ECOLOGY OF WINTERING BLACK-CAPPED VIREOS IN MEXICO

A Dissertation

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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December 2013

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

The black-capped vireo (*Vireo atricapilla*) is an endangered Neotropical migratory songbird that has received considerable attention in its breeding range, but relatively little attention in its winter range in Mexico. To address information needs regarding winter ecology of the black-capped vireo, I conducted research in Mexico focused on investigations of the winter distribution, habitat use, and migratory linkages between breeding and wintering sites.

Over 3 winter periods in 2002–2004, I identified and described the geographic distribution for the black-capped vireo at study sites across 8 states in western Mexico and determined if differential migration occurs among different classes of individuals. I documented winter occupancy in the 5 most northern Mexican states surveyed (Sinaloa, Durango, Nayarit, Jalisco, and Colima), and identified a strong association between sex/age class and winter latitude with adult males occupying habitat at more northern latitudes relative to females and juveniles.

During two winters in 2003-2004, I conducted field research at study sites in Mexico to evaluate patterns of winter habitat use by black-capped vireos and determine which habitat characteristics may influence vireo use of winter patches. Winter habitat use by black-capped vireos was best predicted by increasing values of slope and foliage cover, and by decreasing values of canopy cover and tree diameter. Vireo use plots characterized as thorn forest had greater foliage density, greater shrub density, less canopy cover, and smaller tree diameter than plots classified as tropical deciduous or

semi-deciduous forest, suggesting that thorn forests may be most suitable for vireo occupancy during the winter months.

I also used stable carbon, hydrogen, and nitrogen isotopes in black-capped vireo feathers obtained across 3 states in the breeding range and 8 states in the wintering range to determine if vireo feathers collected on the wintering grounds could be used to assess breeding origins and to determine if a relationship exists between breeding and wintering latitudes such as chain or leapfrog migration. Feathers collected at both breeding and wintering sites displayed considerable variability in isotopic composition for all 3 isotopes analyzed, and thus did not provide sufficient information to establish migratory linkages between breeding and wintering sites.

DEDICATION

To my family

Mom
For your unwavering love and support in all that I do

Dad
For wanting this for me, I wish you could still be here

Marilyn
For the happiness you bring to me

ACKNOWLEDGEMENTS

I sincerely appreciate the generous financial support for this research provided by the U.S. Fish and Wildlife Service (USFWS) and Texas Parks and Wildlife Department (TPWD). I especially thank Dr. Craig Farquhar of TPWD who first envisioned a study of vireos in Mexico and who was instrumental in many ways in getting this project off the ground. Thanks as well to the Departments of Wildlife and Fisheries Sciences (WFSC), Biology, and Rangeland Ecology and Management (now Ecosystem Science and Management; ESSM), as well as the Texas Wildlife and Fisheries Sciences Extension Unit who all have employed me at various times throughout my time at Texas A&M University (TAMU). I also wish to acknowledge the USFWS Migratory Bird Permit Office, the USFWS Division of Management Authority, and the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) for permits, as well as Dr. Felipe Chavez-Ramirez for granting me use of his bird banding permit.

I am indebted to Dr. José Ignacio "Nacho" González and Oscar Ballesteros at the Universidad Autónoma de Nuevo León for storing feathers for me, obtaining expert permits, and for assistance with preparing and exporting the feathers across the border. To Dr. Xico Vega of PRONATURA and the Universidad Autónoma de Sinaloa, I appreciate the access they provided to La Reserva Ecológica del Mineral de Nuestra Señora in Cosalá, Sinaloa. I extend my gratitude as well to Marcela Ley from PRONATURA and her team of young biologists who accompanied us to the Reserve,

provided campsites, food, and entertainment. My gratitude extends as well to Dr. Eduardo Santana Castellón for access to la Reserva de la Biosfera Sierra de Manantlán.

I am grateful to the generous research museums and collections that provided feather tissues for isotopic analysis. The staff and museums to which I owe my thanks include Dr. Carla Cicero at the University of California, Berkeley Museum of Vertebrate Zoology, Mark Blair Robbins at the University of Kansas Natural History Museum, Paul Sweet at the American Museum of Natural History, Dr. David Willard at the Field Museum of Natural History, Gene Hess at the Delaware Museum of Natural History, Dr. John Hafner at the Moore Laboratory of Zoology at Occidental College, Dr. Robert Prys-Jones at the British Museum of Natural History, and Dr. Gary Graves at the Smithsonian Institution National Museum of Natural History. I also owe tremendous gratitude to Dr. David Cimprich of The Nature Conservancy and Dr. Joseph Grzybowski of the University of Central Oklahoma, who collected and provided feather samples from Fort Hood, Texas, and Fort Sill, Oklahoma, respectively.

The Colorado Plateau Stable Isotope Laboratory (CPSIL) in Flagstaff, Arizona conducted the feather isotope analyses for me, and I am indebted to Richard Doucett of CPSIL for his guidance and cooperation. I appreciate the cooperation of Leslie Schwierzke Wade, Reagan Errera, and Carrie Miller in Dr. Dan Roelke's laboratory in WFSC at TAMU for access to space and equipment used for preparation of feather tissues for isotopic analysis.

I am forever grateful to my field assistants Chris Merkord, Jennifer Reidy, and Chris Burney, who accompanied me to Mexico and each contributed tremendously to the

success of the project. Others who were helpful in various aspects of this research include Dr. Keith Hobson with Environment Canada, who generously provided his time for conversations about my isotope research, particularly in helping trying to understand some of the problems I encountered with my results. Dr. Miguel Mora of WFSC also provided useful feedback on the isotope data and other aspects of my research. To the many bird enthusiasts on listservs who provided tips as to where to look for black-capped vireos in Mexico, I owe my sincere gratitude. Also, I greatly appreciate the generosity of the expatriates in Mexico who were interested in my project, particularly Ben Wassink who was a local guru on the birds around Laguna Santa Maria del Oro in Nayarit. He and others at Koala Bungalows often provided us food and good company as well. To the people of Mexico, I cannot express enough how much I admire and appreciate your generosity and goodwill.

I would like to thank the members of my committee for their guidance and support throughout the course of my research, including Dr. Douglas Slack (WFSC), Dr. Bill Grant (WFSC), Dr. Neal Wilkins (WFSC), and Dr. Ben Wu (ESSM). I particularly want to express my gratitude towards Dr. Slack, who in addition to being my Committee Chair, I also consider a friend, colleague, and mentor. The education he provided me extends far beyond this dissertation or any coursework. Staff of WFSC at TAMU helped keep me on track throughout my studies; I thank all of them, especially Vicki Buckbee, Shirley Konecny, and Diann Radke.

Thanks also to my many friends and colleagues at TAMU who have made my time here a terrific experience. I owe a debt of thanks to each of my lab mates in the

Slack lab for their friendship, humor, advice, and much more, including April Conkey, Danielle Rutka Greer, Dan Kim, Kristin Millenbach LaFever, Glenn Proudfoot, Dawn Sherry, Tsuyoshi Watanabe, and Laura Weber. I also wish to thank Glenn for his tremendous assistance with preparing and building various pieces of equipment for my fieldwork in Mexico. I appreciate the assistance provided by Heather Mathewson, Paige Schmidt, and Tiffany McFarland with other aspects of my research. The list of friends who have provided me friendship while at TAMU is lengthy, but in addition to my lab mates and others mentioned above, other friends I wish to thank include Kevin Baker, Lindsay Bennett, Meg Byerly, Thomas Dixon, Lance and Eve Fontaine, Richard Heilbrun, Christian Kaufman, David LaFever, Eddie Lyons, Anna Munoz, Dean Ransom, Christa Iacono Ruffins, Angela Skeeles-Worley, Stacey Allison Steinbach, and Holly Stephens.

I especially thank my family for their unconditional love, support, patience, and encouragement. Thank you to my mother, Mary Craig Powell, my brother John, his wife Wendy, and their daughter Rebecca. Thank you to my dogs Maggie (now deceased) and Scout, who were always by my side. Finally, thank you to Marilyn Stone for your love and encouragement; you truly are special to me.

NOMENCLATURE

‰	Per mil
$\delta^{13}C$	Stable carbon isotope
$\delta^{2}H$	Stable hydrogen isotope (deuterium)
$\delta^{15}N$	Stable nitrogen isotope
AIC_c	Akaike's Information Criterion for small sample sizes
ANOVA	Analysis of variance
ASP	Slope aspect
$\hat{\beta}$	Model parameter estimate
CAM	Crassulacean acid metabolism
CI	Confidence interval
COA	Coahuila
COL	Colima
CnCv	Canopy cover
CPSIL	Colorado Plateau Stable Isotope Laboratory
DBH	Diameter at breast height
DUR	Durango
ESA	Endangered Species Act
F	F-ratio
FD	Vertical foliage density
GNIP	Global Network for Isotopes in Precipitation

GPS	Global Positioning System
GUE	Guerrero
ha	Hectare
JAL	Jalisco
LSD	Least significant difference
MIC	Michoacán
NAY	Nayarit
OAX	Oaxaca
OKL	Oklahoma
ORNIS	Ornithological Information System
P	P-value
SE	Standard error
SEMARNAT	Secretaría de Medio Ambiente y Recursos Naturales
ShDis	Mean distance to nearest shrub within plot
SIN	Sinaloa
TEX	Texas
TPWD	Texas Parks and Wildlife Department
TrDis	Mean distance to nearest tree within plot
USFWS	United States Fish & Wildlife Service
UV	Ultraviolet
w_i	Akaike weights
$\bar{x}$	Mean

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CHAPTER I

INTRODUCTION

The black-capped vireo (*Vireo atricapilla*) is a small, migratory Neotropical songbird 10 to 12 cm long (Graber 1957, Grzybowski 1995, Howell and Webb 1995) that is considered unique among vireos in being sexually dichromatic (Graber 1957) and in showing delayed plumage maturation in first-year males (Rohwer et al. 1980; Wilkins et al. 2007). Mature males have a black crown and upper half of the head, a mostly olive green back, white underparts, and greenish-yellow flanks (Oberholser 1974, Campbell 1995), while females are similar in appearance but duller and with a slate gray head (USFWS 1991, Campbell 1995, Grzybowski 1995). Black-capped vireos have a black bill, spectacles formed by a partial white eye-ring that connects with their white lores, and eyes that are red in mature males and brownish-red or amber in females and immature birds (Graber 1957, Howell and Webb 1995, Pyle 1997).

The black-capped vireo was federally listed as Endangered in 1987 under the Endangered Species Act (ESA) of 1973, as amended (Ratzlaff 1987). At the time of listing, the primary threats identified for the species included habitat loss from development, habitat destruction from the grazing of sheep, goats and exotic livestock, and nest parasitism by brown-headed cowbirds (*Molothrus ater*; Ratzlaff 1987). U.S. Fish and Wildlife Service (1991) developed a Recovery Plan, but did not designate critical habitat. A 5-year Status Review was completed by Wilkins et al. (2006) that documented a known population size of 6,269 individuals compared to only 191 pairs at the time of listing (Marshall et al. 1985). More recent efforts have focused on applying a

rigorous study design to the analysis of distribution and abundance of black-capped vireo across their breeding range in Texas (McFarland et al. 2012, 2013). Based on information provided in the review by Wilkins et al. (2006), the U.S. Fish and Wildlife Service (USFWS 2007) concluded that the overall threat level to the black-capped vireo is less in magnitude than it was at the time the species was listed and thus recommended downlisting the species to Threatened status under the ESA.

The historic breeding range of the black-capped vireo purportedly included portions of Kansas, Oklahoma, Texas and north-central Coahuila, Mexico (Shull 1986). Today, the only known viable population of black-capped vireos in Oklahoma occurs in Comanche County, where both Fort Sill Military Reservation and Wichita Mountains National Wildlife Refuge actively manage for the species. The southern limits of the known breeding range now extend farther south than was previously known.

Historically, central Coahuila was considered the southern limits of the breeding range (Renardo 1886, Moore 1938, Miller 1955, Van Hoose 1955, Graber 1961, Wauer and Ligon 1977, Benson and Benson 1990), although there were some unconfirmed single records from Tamaulipas (Phillips 1911), San Luis Potosi (Davis *in* Graber 1961), and Nuevo León (compiled in Marshall et al. 1984 and Marshall et al. 1985). Recently, however, the first confirmed record of black-capped vireos breeding in Mexico outside of Coahuila came from central Nuevo León (Bustamante) and in southwestern Tamaulipas (Palmillas; Farquhar and Gonzalez 2005). Contreras-Balderas et al. (2012) also reported recently on breeding black-capped vireos in Nuevo León. Approximately 20 adult black-capped vireos and four fledglings found in Tamaulipas are at least 700

km south of the previous confirmed southernmost records from Coahuila (Farquhar and Gonzalez 2005), thus extending the known breeding range in Mexico considerably further south than what was previously known (Fig. 1.1).

The winter range is thought to include the Pacific slopes of the Sierra Madre Occidental Mountains in Mexico, extending from southern Sonora to Oaxaca (Fig. 1.1). Location records during the winter period include the Mexican states of Sonora (Russell and Morrison 1996), Sinaloa (Graber 1957, 1961, Marshall et al. 1985, Howell 1999, Gonzalez-Medina et al. 2009), Durango (Graber 1957, Howell and Webb 1995), Nayarit (Davis 1960, Schaldach 1963, Marshall et al. 1985, Howell 1999), Jalisco (Hutto 1992, 1994, Howell 1999), Colima (Howell 1999), Michoacán (Howell and Webb 1995, MacGregor-Fors et al. 2012), Mexico (probable migrant collected in September; Escalona et al. 1995), Hidalgo (probable migrant seen in mid-October; Marshall et al. 1985), Guerrero (Howell and Webb 1995), and Oaxaca (Binford 1989, Howell 1999). Most winter records come from either Sinaloa and Nayarit, the two states that Graber (1961) described as the center of the wintering grounds. However, these observations are mostly incidental and the ones focused specifically on black-capped vireos (e.g., Graber 1957, 1961, Marshall et al. 1985) were limited in extent and duration. To date, there have been no systematic studies of black-capped vireos across their winter range.

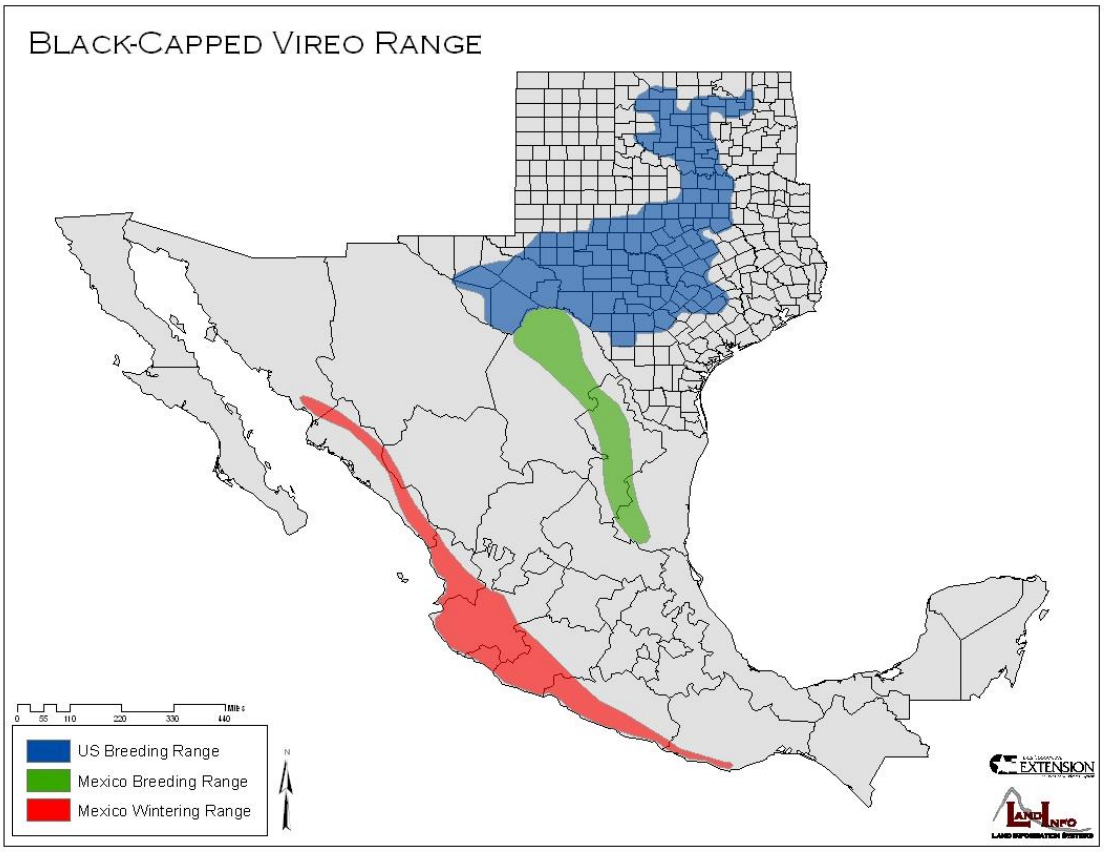

Figure 1.1. Currently known breeding and wintering ranges for the black-capped vireo. Ranges are generalized for all known locations since time of listing (Wilkins et al. 2006).

Graber (1957, 1961) qualitatively assessed wintering habitat as complex and somewhat aberrant. Based on her observations, vireos selected both arid scrub 0.75 to 3 m in height (southern Sinaloa) and mesic secondary growth with high plant diversity originating from widespread clearing (coastal Nayarit). To date, no researcher has quantitatively evaluated black-capped vireo winter habitat.

Connectivity between events on the breeding grounds and the wintering grounds has important consequences for the ecology, evolution and conservation of Neotropical migratory birds (Myers et al. 1987, Sherry and Holmes 1995, Webster et al. 2002, Webster and Marra 2005, Faaborg et al. 2010). Individual birds carry over effects between seasons, such as physical condition or date of arrival, that can explain variation in reproductive success and annual survival (Gill et al. 2001, Harrison et al. 2011, Alves et al. 2013). In order to understand how the biology of a species is influenced by the interactions of events on both the breeding and nonbreeding grounds, it is necessary to track populations or individuals between different phases of the life cycle. One innovative approach that avoids many of the drawbacks of conventional tracking techniques involves stable isotope analysis of bird feathers. Many species of migratory songbirds grow feathers on or close to their breeding grounds before fall migration. Feathers are metabolically inert and maintain an isotopic record reflecting the location where the tissue was synthesized (Mizutani et al. 1990). Therefore, a feather collected on the wintering grounds would reflect the isotopic record during the breeding season (period of growth), allowing researchers to effectively link these two areas (e.g., Hobson and Clark 1992, Chamberlain et al. 1997, Wassenaar and Hobson 2000, Rubinstein et al.

2002, Norris et al. 2006). To date, no researcher has analyzed stable isotopes in black-capped vireo feathers to determine migratory linkages between breeding and wintering populations.

The black-capped vireo has received considerable attention in its breeding range (e.g., Graber 1961, Marshall et al. 1985, U.S. Fish and Wildlife Service 1991, Grzybowski 1995, Wilkins et al. 2006), and all of the major threats described for this species at the time of listing related to the breeding grounds (Ratzlaff 1987). Much less is known about this species in its non-breeding (winter) range, and this knowledge gap is cited as one of the top research priorities in both the Black-capped Vireo Recovery Plan (U.S. Fish and Wildlife Service 1991) and the Black-capped Vireo Population and Habitat Viability Assessment Report (U.S. Fish and Wildlife Service 1996).

Research Objectives

My primary research goal was to gain a better understanding of the winter ecology of the endangered black-capped vireo in Mexico through investigations of winter distribution, habitat use, and migratory linkages between breeding and wintering sites. Three stand-alone studies (described here in Chapters II-IV) were designed to attain this goal. In Chapter II, I report on patterns of geographic distribution of the species at sites across western Mexico and report evidence on latitudinal sexual segregation of black-capped vireos in the winter range. In Chapter III, I describe patterns of habitat use by black-capped vireos in the winter range. In Chapter IV, I discuss attempts to link black-capped vireo breeding and wintering grounds by use of stable isotope analysis of

feathers collected across both the breeding and wintering grounds. Lastly, Chapter V summarizes the findings of earlier chapters and discusses implications for our understanding of the ecology and conservation of black-capped vireos.

In Chapter II, the study objectives were:

1. Identify and describe the geographic distribution for the black-capped vireo during the winter period in western Mexico.
2. Determine if differential migration occurs among different classes of individuals.
3. Compare patterns of latitudinal segregation among different species of North American vireos.
4. Evaluate body condition of black-capped vireos among different classes of individuals as a measure of differences in availability and quality of food across different geographic locations on the Mexican wintering grounds.

In Chapter III, the study objectives were:

1. Describe habitat characteristics of winter patches used by black-capped vireos.
2. Determine what habitat characteristics may influence vireo use of winter patches.
3. Evaluate differences in habitat characteristics between winter patches across different latitudes, elevations, and habitat types at sites across western Mexico, as well as between different age/sex classes.

In Chapter IV, the study objectives were:

1. Determine if breeding latitude was related to stable hydrogen isotope ratio in black-capped vireo feathers.
2. Determine if feathers collected on the wintering grounds could be used to assess the breeding origins of black-capped vireos.
3. Determine if a relationship exists between breeding and wintering latitudes (e.g., chain or leapfrog migration).

CHAPTER II

GEOGRAPHIC DISTRIBUTION AND DIFFERENTIAL MIGRATION OF BLACK-CAPPED VIREOS IN THE WINTER RANGE

Synopsis

It is important to gain a better understanding of the winter distribution of the black-capped vireo in order to understand how its winter ecology may influence events during other periods of its annual life cycle, identify potential threats to the species, and detect differences in distribution among population classes. Differential migration occurs when different age or sex classes segregate along a latitudinal gradient during the nonbreeding period. In this study, I identified and described the geographic distribution for the black-capped vireo in western Mexico over 3 winter periods in 2002–2004 and determined if differential migration occurs among different classes of individuals. The black-capped vireo is considered the only sexually dimorphic species of vireo; because sexually dimorphic species are more likely than monomorphic species to exhibit latitudinal sexual segregation (a form of differential migration), I also compared patterns of latitudinal segregation among 12 species of North American vireos using museum specimen data. This was the first systematic study of black-capped vireo winter occupancy across the winter range, and I documented winter occupancy in the states of Sinaloa, Durango, Nayarit, Jalisco, and Colima. I found a strong association between sex/age class and winter latitude whereby adult males occupied habitat at more northern latitudes and females and juveniles occupied habitat at more southern latitudes. The

analysis of museum specimen data provided additional evidence of latitudinal segregation by sex among wintering black-capped vireos. My analysis of museum specimens also provided evidence of latitudinal sexual segregation among Bell's vireo (*V. bellii*), red-eyed vireo (*V. olivaceus*), and yellow-throated vireo (*V. flavifrons*), which was not expected because those species are not considered sexually dimorphic. The present study found female black-capped vireos migrating further than males, which may result in higher mortality rates among females and explain male-biased adult sex ratios, which ultimately may have led to the evolution of sexual dichromatism in the species. Differential migration also may explain protandry among black-capped vireos, the earlier arrival of males relative to conspecific females at the breeding grounds, which has many other potential implications for the ecology and conservation of the species.

Introduction

Historically, black-capped vireo breeding populations occupied at least 22 counties in Oklahoma, 69 counties in Texas, and 1 Mexican state (Coahuila), but much of the former breeding range is no longer occupied by vireos, with recent evidence suggesting occupancy in no more than 3 counties in Oklahoma, 38 counties in Texas, and 3 states in Mexico (Coahuila, Nuevo León, Tamaulipas; Wilkins et al. 2006). The most recent estimate of known population size for the black-capped vireo across its range is 6,289 individuals (Wilkins et al. 2006), and the vireo is federally listed as an endangered species (Ratzlaff 1987). The primary threats supporting the decision to list the species pertained to factors during the breeding season, including habitat loss from

development, nest parasitism by brown-headed cowbirds, and habitat destruction from livestock grazing (Ratzlaff 1987).

However, the black-capped vireo spends over half its annual life cycle either in migratory transit or on its non-breeding (winter) grounds in Mexico, and little is known about this period of the species' life cycle. As with many other species, the vireo is likely as vulnerable to threats during the winter period as during the breeding period. Although most efforts to understand population dynamics of Neotropical migratory songbirds have focused on the relatively short period of breeding in temperate or boreal climates, researchers have increasingly recognized the importance of the nonbreeding season, a longer period of self-maintenance and survival in tropical and semi-tropical habitats (Parrish and Sherry 1994, Faaborg et al. 2010, Rockwell et al. 2012).

Little information is available concerning the winter distribution and ecology of the black-capped vireo, which is thought to occur along the Pacific slopes of the Sierra Madre Occidental Mountains in Mexico, extending from southern Sonora to Oaxaca (Fig. 1.1; Wilkins et al. 2006). Recently, Gonzalez-Medina et al. (2009) studied the winter ecology and distribution of the black-capped vireo in Sinaloa. Two previous studies on black-capped vireos partially focused on winter ecology (Graber 1961, Marshall et al. 1985), but the Mexico portions of these studies were mostly qualitative and were limited in duration (each conducted over a period of weeks during a single season) and geographic scope (each conducted only in Sinaloa and Nayarit).

All other known information concerning the distribution of the black-capped vireo during winter is anecdotal, coming from general descriptions or location records in

bird guides or bird survey reports. Based on this limited information, known records of black-capped vireos during winter come from the Mexican states of Sonora (Russell and Morrison 1996), Sinaloa (Graber 1957, 1961, Marshall et al. 1985, Howell 1999, Gonzalez-Medina et al. 2009), Durango (Graber 1957, Howell and Webb 1995), Nayarit (Davis 1960, Schaldach 1963, Marshall et al. 1985, Howell 1999), Jalisco (Hutto 1992, 1994, Howell 1999), Colima (Howell 1999), Michoacán (Howell and Webb 1995), Mexico (Escalona et al. 1995), Hidalgo (Marshall et al. 1985), Guerrero (Howell and Webb 1995), and Oaxaca (Binford 1989, Howell 1999, Vega Rivera et al. 2010). The single records from the states of Mexico and Hidalgo are probable migrants because they were collected in September and mid-October, respectively, as may be the 2 observations from Sonora that occurred during November. With the exception of Sonora and Hidalgo, there are also specimen records from the same states, most of which are concentrated in Sinaloa and Nayarit. For example, 81% of all winter-season black-capped vireo specimen records from Mexico in the ORNIS (Ornithological Information System) database (http://ornisnet.org/) are from either Sinaloa or Nayarit.

Based on a review of existing location records, Graber (1961) described Sinaloa and Nayarit as the center of the winter range for the species, although Schaldach (1963) stated that the species likely only occasionally winters in Nayarit. Recent modeling of the potential winter distribution of the black-capped vireo by Vega Rivera et al. (2010) predicted a range including all the states proposed by Wilkins et al. (2006) as the winter distribution (from Sonora in the north through Oaxaca in the south), but also extending further north, south, and inland (eastward), particularly in the southern states of Oaxaca

and Guerrero. Defining both the extent of the vireo's winter range and the proportional usage within that range is critical to understanding potential threats to the species.

An analysis of wintering distributions also may reveal other differences between demographic classes of the population (e.g., ages, sexes) that have important ecological and conservation implications. Habitats used by migratory birds during the winter may vary in quality, as evident by examples of winter territorial behavior and site tenacity (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989, Holmes and Sherry 1992), habitat-specific variations in overwinter site persistence (Greenberg 1992), sexual differences in winter habitat use (Lynch et al. 1985, Morton et al. 1987, Morton 1990, Wunderle 1992, Parrish and Sherry 1994), and experimental evidence of nonbreeding habitat competition (Marra et al. 1993).

One factor contributing to variation in habitat quality between winter sites is resource seasonality (Parrish and Sherry 1994, Rockwell et al. 2012). Rainfall is strongly seasonal in the northern Neotropics where most Neotropical migrants winter (Terborgh 1989, Smith et al. 2010, 2011), and seasonal rainfall patterns may influence resource abundance and foraging opportunities for birds (Schwartz 1980, Karr and Freemark 1983, Lefebvre et al. 1992, Poulin et al. 1992, Smith et al. 2011). Food availability in winter tends to limit population size of migratory birds via winter habitat quality; prey abundance declines in the late-winter dry season, accompanied by a simultaneous deterioration of body condition, and decreased survival or persistence both in drought-stressed habitats and in relatively dry winters (reviewed in Sherry et al. 2005). Thus, food availability is probably the primary driver of habitat suitability for

migratory birds in winter (Hutto 1985, Greenberg 1986, Leisler 1990, Parrish and Sherry 1994), but it is severely limited by the winter dry season in much of the northern Neotropics (Orejuela et al. 1980, Schwartz 1980, Karr and Freemark 1983).

In addition to food availability, other mechanisms of population limitation in wintering migrant birds may be important. For example, competition with resident birds or other migrant species may also be a factor. Greenberg (1986, 1995) proposed that wintering migrant birds compete diffusely with resident birds for food and resident species displace migrants from the best local breeding habitats (i.e., those with greater proportions of protein-rich larger invertebrates). Additionally, animals in poor body condition due to food shortages may be more susceptible to predators and parasites (reviewed in Sherry et al. 2005).

Differential migration may occur among long-distance migratory birds, whereby the distance travelled during migration may vary among individuals, with different age or sex classes segregating along a latitudinal gradient during the nonbreeding period (Myers 1981, Gauthreaux 1982, Ketterson and Nolan 1983, Terrill and Able 1988). The most typical pattern of differential migration involves females migrating farther than males and juveniles migrating farther than adults (reviewed in Cristol et al. 1999). Several researchers have described long-distance migrants that exhibit latitudinal sexual segregation on the wintering grounds, whereby males winter farther north than females (Howell 1953, Johnston 1970, Vidal et al. 1994, Sherry and Holmes 1997), including 8 species that winter in Mexico (Komar et al. 2005). Distinct winter distributional

differences between sex or age classes are known to occur for at least 53 species and possibly over 100 more (Cristol et al. 1999).

Sexual segregation during the nonbreeding period may occur more frequently among sexually dimorphic species (dimorphism is the difference in coloration of males and females within a species) than among monomorphic species (Marra and Holmes 2001). Latitudinal segregation may ultimately lead to sexual dichromatism if females winter in less optimal locations than males, resulting in poor body condition and lower survivorship relative to males. The imbalance in survivorship between males and females skews adult sex ratios towards more males, leading to intense male competition over females for breeding, which may involve the development of brighter plumage, ultimately resulting in sexual dichromatism (Marra and Holmes 2001).

Thus, different classes of individuals within a population may segregate during the winter, the extent of which may have important ecological implications for migratory songbirds. For example, classes of individuals of a spatially segregated population may experience different ecological conditions during the winter, such as varying degrees of interspecific competition, predation, inclement weather, and food scarcity, all of which may affect survivorship (Cristol et al. 1999). If differential migration results in different annual survival rates between sex or age groups or the evolution of different habitat preferences, these patterns may have implications for conservation or management efforts (Komar et al. 2005). For example, management may need to focus on separate wintering areas for males and females if sexual segregation occurs on the wintering grounds, as Vidal et al. (1994) suggested for the golden-cheeked warbler (*Dendroica*

chrysoparia). A landscape approach to conservation of the wintering grounds may be valuable if different classes of individuals in the population occupy separate geographic locations (Askins 2000, Sherry et al. 2005).

Specific objectives for this study were (1) to identify and describe the geographic distribution for the black-capped vireo during the winter period in western Mexico, and (2) to determine if differential migration occurs among different classes of individuals. Because the black-capped vireo is considered the only sexually dimorphic species of vireo (Graber 1957, Grzybowski 1995) and because sexually dimorphic species are more likely than monomorphic species to exhibit latitudinal sexual segregation (Marra and Holmes 2001), (3) I also compare patterns of latitudinal segregation among different species of North American vireos. Finally, (4) I compare body condition between adult male vireos and female and young vireos as a measure of possible differences in availability and quality of food between classes of individuals in a latitudinally segregated population that spend the winter in different geographic locations.

Methods

Study Location

Field research was conducted over 3 winter periods in 2002–2004 (27 January 2002 – 11 April 2002; 31 January 2003 – 9 April 2003; 7 December 2003 – 19 March 2004) at study sites located along the Pacific slopes of the Sierra Madre Occidental mountains in western Mexico, and ranging in elevation from sea level to 1500 m (Fig.

2.1, Table 2.1). Sites were located in the states of Sinaloa, Durango, Nayarit, Jalisco, Colima, Guerrero, Michoacán, and Oaxaca.

The 3 broadly defined categories of forest within the Sierra Madre Occidental include thorn forest, tropical deciduous and semi-deciduous forest, and pine-oak forest (Miranda and Hernandez 1963, Rzedowski 1978, Ricker et al. 2007). Thorn forest grows in more arid regions at lower altitudes near the coast, whereas deciduous and semi-deciduous forests grow on the relatively more humid hills below the pine-oak woodlands, which occur at higher altitudes (Fig. 2.2; Arbingast et al. 1975).

Thorn forest, tropical deciduous forest, and tropical semi-deciduous forest all fall within the general classification of tropical dry forest (also called seasonally dry tropical forest). Mexico's tropical dry forests are found in dry to sub-humid climates (annual average rainfall 600-1200 mm) that are warm (annual average temperature 20-29 degrees Celsius) with highly marked seasonality (5- to 8-month dry season), and that occur at altitudes of 0-1500 m (Miranda and Hernandez 1963, Rzedowski 1978, Trejo 1999, Sanchez-Azofeifa et al. 2005). These forests are typically dominated by deciduous trees (more than 50%) and are predominantly established on moderate to steep slopes with shallow soils (Trejo and Dirzo 2002, Sanchez-Azofeifa et al. 2005).

Study sites included all 3 of the primary vegetation associations (i.e., thorn forest, tropical deciduous and semi-deciduous forest, and pine-oak forest) along the western slopes of the Sierra Madre Occidental, although survey effort was not distributed equally among them because the relative areas of each vegetation association are not equal, access to each association is not equally reliable (e.g., roads are more

Figure 2.1. Map of Mexico depicting locations of study sites where black-capped vireos were found (stars) and those where vireos were not found (circles).

Table 2.1. Location of study sites surveyed for black-capped vireos in Mexico. Site names match those in Fig. 2.1 and are arranged north to south. Elevations are approximate.

Study Site	State	Elevation (m)
El Fuerte	Sinaloa	100
Culiacán	Sinaloa	25
Cosalá	Sinaloa/Durango	400
Mazatlan	Sinaloa	180
Copala	Sinaloa	550
San Blas	Nayarit	200
Cerro de San Juan	Nayarit	1100
Santa María del Oro	Nayarit	780
Tequila	Jalisco	1200
Sayulita	Nayarit	30
Puerto Vallarta	Jalisco	10
Chapala	Jalisco	1500
Autlan (Sierra de Manantlán)	Jalisco	1500
Comala	Colima	1400
Uruapan	Michoacán	1600
Barranca el Choncho	Jalisco	400
Playa de Oro	Colima	120
Playa Azul	Michoacán	10
Zihuatanejo	Guerrero	20
Chilpancingo	Guerrero	1250
Atoyac	Guerrero	250
Oaxaca	Oaxaca	1550
Puerto Escondido	Oaxaca	60
Puerto Ángel	Oaxaca	20

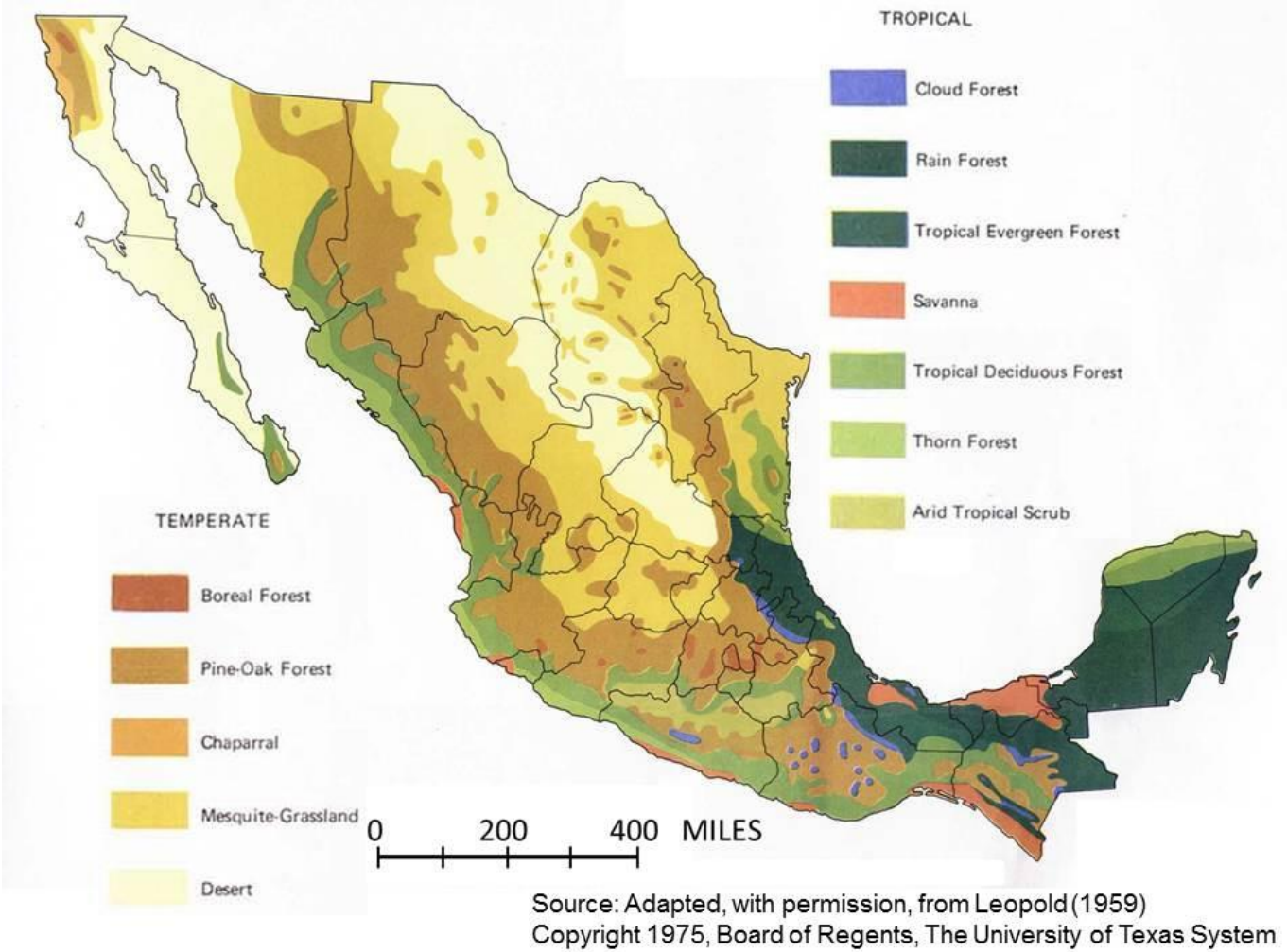

Figure 2.2. The primary vegetation zones of Mexico, including thorn forest, tropical deciduous forest, and pine-oak forest zones along the Pacific Coast (After Arbingast et al. 1975).

accessible at the lower elevations where human populations are found relative to higher elevation pine-oak forests), and because vireos were not expected to occur equally among the vegetation associations. Most sites have been disturbed to some degree by human activities. Tropical dry forest frequently occurs in a mosaic of disturbed secondary vegetation and patches of relatively undisturbed primary vegetation (Trejo and Dirzo 2000, Gordon et al. 2004, Gove et al. 2005).

Data Collection

To evaluate patterns of differential migration among demographic classes of black-capped vireos, I conducted field investigations of wintering vireos in Mexico across three winters (2002-2004), and also examined data from museum specimens collected across the winter range of the species. Because of the large extent of the region surveyed, the relative scarcity of the endangered focal species, and the relative lack of information about existing winter populations, survey sites in many cases were located at sites of potential occurrence based on the literature (e.g., Graber 1961, Marshall et al. 1985, Binford 1989, Hutto 1992, Howell and Webb 1995, Howell 1999) or from amateur and professional birding trip reports. At study sites, I walked through scrub or forested habitats searching visually for individual black-capped vireos and also seeking auditory clues to their presence, including vocalizations by vireos and members of mixed-species flocks that sometimes associate loosely with black-capped vireos. This approach has been used for winter studies of golden-cheeked warblers, a species in which winter vocalizations by the species are infrequent (e.g., Rappole et al. 1999,

2000). Black-capped vireos tend to be among the least audible and detectable species, and are not active flock participants, but sometimes appear in the vicinity of winter flocks as non-obligate flock associates. Typical flock members include Wilson's warbler (*Wilsonia pusilla*), blue-gray gnatcatcher (*Polioptila caerulea*), MacGillivray's warbler (*Oporornis tolmiei*), Nashville warbler (*Vermivora ruficapilla*), orange-crowned warbler (*Vermivora celata*), plumbeous vireo (*Vireo plumbeous*), warbling vireo (*Vireo gilvus*), and varied bunting (*Passerina versicolor).* Gonzalez-Medina et al. (2009) most often found black-capped vireos to be solitary, but when other species were present, they included orange-crowned warblers, Wilson's warblers, and warbling vireos.

Once black-capped vireos were initially identified during surveys, I recorded geographic coordinates and elevation of the initial observation point as determined with a global positioning system (GPS). All geographic coordinates were converted from degrees, minutes, and seconds into decimal degrees for statistical analysis.

An accurate classification of wintering black-capped vireo individuals by age and sex was not possible because most individuals cannot be reliably aged or sexed in the field using standard plumage characteristics during much of the nonbreeding winter months (Pyle 1997, S. Howell personal communication). In general, little information exists on black-capped vireo molting patterns (Pyle 1997, Butler et al. 2008). According to Pyle (1997), discrimination between second year, after hatch year, and after second year birds is difficult during the winter months, but discrimination between adult birds (i.e., second year, after hatch year, and after second year birds) and juveniles (i.e., both juvenile and hatch year birds) is reliable. Additionally, sexing birds is not reliable for

second year or after hatch year adults, but is for after second year adult birds (Pyle 1997). Based on these considerations, I conservatively classified black-capped vireos as adults or juveniles, and among adult birds, I classified them as either adult males or unknown. Gonzalez-Medina et al. (2009) used an identical approach in their study of black-capped vireos in Sinaloa. For all statistical comparisons, I compared adult male vireos versus all others (females and juveniles).

The black-capped vireo is considered the only sexually dimorphic species of vireo (Graber 1957, Grzybowski 1995); because latitudinal sexual segregation should occur more frequently among sexually dimorphic species than among monomorphic species (Marra and Holmes 2001), I compared patterns of latitudinal segregation among different species of North American vireos. If latitudinal sexual segregation is more common among sexually dimorphic species, then the black-capped vireo should be the only vireo species to exhibit this pattern.

To examine differences in patterns of latitudinal segregation between black-capped vireos and other vireo species, I compiled a database of location records from museum specimens for the 12 species of long-distance migratory vireos that breed north of Mexico (Barlow 1980). The majority of specimen records do not include information about age class, so this analysis was restricted to latitudinal segregation by sex. I acquired specimen data using the ORNIS database for the following institutions: the Academy of Natural Sciences, American Museum of Natural History, California Academy of Sciences, Cornell University Museum of Vertebrates, Delaware Museum of Natural History, Fort Hays State University Sternberg Museum of Natural History, Los

Angeles County Museum of Natural History, Michigan State University Museum, San Diego Natural History Museum, San Noble Oklahoma Museum of Natural History, Santa Barbara Museum of Natural History, Texas Cooperative Wildlife Collection, Universidad Nacional Autonóma de México, University of Arizona Bird Collection, University of California at Los Angeles Dickey Collection, University of Colorado Museum of Natural History, University of Kansas Natural History Museum, University of Michigan Museum of Zoology, University of Nebraska State Museum, University of Puget Sound James R. Slater Museum of Natural History, Utah Museum of Natural History, University of Washington Burke Museum of Natural History, Washington State University Charles R. Conner Museum, and Yale University Peabody Museum. Additionally, I retrieved specimen data from the websites of other institutions not affiliated with ORNIS, including the Field Museum of Natural History, Harvard University Museum of Comparative Zoology, and the Smithsonian Institution National Museum of Natural History. Finally, I obtained specimen data by request from the Moore Laboratory of Zoology at Occidental College.

From the 29,739 vireo records in this database, I selected only those records that occurred during winter between December and March (to eliminate birds potentially collected during migration), with geographic information describing where the specimen was collected, and that provided information about sex. In some cases, exact latitudinal and longitudinal data were available, but in other cases, geographic data only described relative proximity to a nearby town. For those records without geographic coordinates, I used Google Earth (http://earth.google.com) to determine approximate latitudes of the

collection site (using the geographic coordinates for the center of the nearest town as a standard). Although this method does not provide exact latitudes where specimens were collected, the approximation should be sufficient for the purposes of this study, which is evaluating patterns across large geographic distances. In other words, slight differences in the latitude between the center of a town or some site outside of town, where a specimen was collected, should have negligible effect on an analysis of broad geographic patterns across the hundreds or thousands of miles encompassing a species' winter distribution. The final set of useable specimens with sex, geographic coordinates, and December-March collection dates included 2,438 records of 12 species of vireos.

I evaluated body condition as a measure of nutrition and habitat quality for black-capped vireos captured in the field. Specifically, I measured furcular fat score, an index to body condition, for all black-capped vireos captured in mist nets (e.g., Strong and Sherry 2000, 2001). Upon finding focal black-capped vireos with visual and auditory surveys, birds were captured following standard protocol for mistnetting (Ralph et al. 1993). Fat scoring takes advantage of a bird's thin skin through which subdermal fat deposits can be observed and assessed (Krementz and Pendleton 1990). To measure furcular fat, I used visible fat categories: 0 = none visible, 1 = trace, 2 = fat forming a solid sheet across the bottom of the furculum, and 3 = fat filling furculum (Holmes et al. 1989).

Data Analysis

To evaluate the occurrence of differential migration among different classes of black-capped vireo individuals, I compiled location records from my field investigations

(n = 71) and location records from museum specimens with latitude data (n = 39), and then sorted the records by latitude to test for differences in numbers of adult males versus all others to the north and south of the median latitude (Komar et al. 2005). I compared frequencies of adult males versus all others, north versus south, using contingency-table analysis, with *P*-values determined using a Chi-square test of independence ($\alpha = 0.05$). Specifically, I tested the null hypothesis that there is no association between sex/age class and latitude.

Because it is possible that results from the above analysis may reflect sampling bias (e.g., Komar et al. 2005) instead of real latitudinal differences among classes of individuals, I wanted to further evaluate the strength of differential migration among wintering black-capped vireos. To do so, I divided their locality records into latitudinal quartiles, and tested for differences in numbers of adult males versus all others in the northernmost (i.e., the most northerly 25% of records) and southernmost quartiles (i.e., the most southerly 25% of records; Komar et al. 2005). I again used contingency-table analysis and determined *P*-values with a Chi-square test of independence ($\alpha = 0.05$).

To compare patterns of sexual segregation among different species of vireos, I used the dataset of museum specimen records to evaluate the occurrence of latitudinal segregation by sex among the 12 species of long-distance migratory vireos that breed north of Mexico. For each species, I again sorted the records by latitude and used contingency-table analysis to compare frequencies of males versus females, north versus south of the median latitude, and determined *P*-values with a Chi-square test of

independence ($\alpha = 0.05$). I tested the null hypothesis that there is no association between sex and latitude for each of the 12 species.

I evaluated body condition among wintering black-capped vireos using a Mann-Whitney *U* test, testing for differences in fat scores among adult males versus female and young.

Results

Search effort involved 2,396 observer hours over 3 winter seasons of study in Mexico (Table 2.2). I observed a total of 71 black-capped vireos (9 in 2001–2002, 13 in 2002–2003, 49 in 2003–2004) at study sites located along the Pacific slopes of the Sierra Madre Occidental mountains in western Mexico (Fig. 2.1, Table 2.1, Appendix A). Observations were located in Sinaloa (17), Durango (4), Nayarit (33), Jalisco (3), and Colima (14). No black-capped vireos were found in Guerrero, Michoacán, or Oaxaca. The range of elevations at which black-capped vireos were located was 0-1515 m, with 25 vireos located at 0-400 m elevation, 29 between 400-1000 m elevation, and 17 at elevations greater than 1000m (Appendix A). I trapped 27 black-capped vireos (14 adult males, 13 females and juveniles) in mistnets over the course of the study and evaluated their body condition. I also used data from 29 museum records of black-capped vireos for these analyses.

I found an association between sex/age class and winter latitude using the Chi-square test of independence ($\chi^2 = 16.234$, df = 1, $P < 0.001$; Table 2.3). Adult males occupied winter habitat at more northerly latitudes and females and juveniles occupied

Table 2.2. Search effort for black-capped vireos in Mexico by state and year, measured by number of observer hours.

Winter	SIN[1]	DUR	NAY	JAL	COL	MIC	GUE	OAX	Total
2001-02	51	0	162	125	53	31	51	46	519
2002-03	274	0	270	192	92	0	16	25	869
2003-04	212	6	314	106	175	44	95	56	1008
Total	537	6	746	423	320	75	162	127	2396

[1] Mexican states where fieldwork was conducted include Sinaloa (SIN), Durango (DUR), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacán (MIC), Guerrero (GUE), and Oaxaca (OAX).

Table 2.3. Contingency table for the Chi-square test of independence comparing observed and expected counts of adult male and all other black-capped vireos north and south of the median latitude across the wintering range at sites in western Mexico, 2003–2004. Expected counts are shown in parentheses. The Chi-square test showed an association between sex and winter latitude ($\chi^2 = 16.234$, df = 1, $P < 0.001$).

Sex/Age	North	South	Total
Adult Male	38	18	56
	(28)	(28)	
Female and Young	12	32	44
	(22)	(22)	
Total	50	50	100

winter habitats at more southerly latitudes (Table 2.3, Fig. 2.3). Comparing adult males versus all others between the northernmost and southernmost quartiles, the Chi-square test of independence also showed an association between sex/age class and winter latitude for black-capped vireos ($\chi^2 = 9.680$, df = 1, $P = 0.002$; Table 2.4), which provides additional evidence that adult male vireos occupy winter habitats at more northerly latitudes and females and juveniles occupy winter habitat at more southerly latitudes.

The analysis of museum locality records for 12 species of North American migratory vireos revealed significant patterns of sexual segregation for 5 species of vireo (Table 2.5). The Chi-square test of independence showed there was an association between sex and winter latitude for black-capped vireo, Bell's vireo (*V. bellii*), plumbeous vireo, red-eyed vireo (*V. olivaceus*), and yellow-throated vireo (*V. flavifrons*). Caution in interpretation of data for gray vireo (*V. vicinior*) and plumbeous vireo is warranted because of low sample sizes. In the Chi-square test of independence, both of these species had expected frequencies of less than 5 for more than 20% of the cells in the contingency table, which may be inadequate for producing reliable Chi-square approximations (Agresti 2007).

Body condition (i.e., fat scores) tended to be higher for adult male vireos (mean = 1.71, SE = 0.29, n = 14) than for female and young birds (mean = 1.38, SE = 0.35, n = 13), although the difference was not statistically significant (Mann-Whitney $U = 73.00$, P = 0.360 two-tailed).

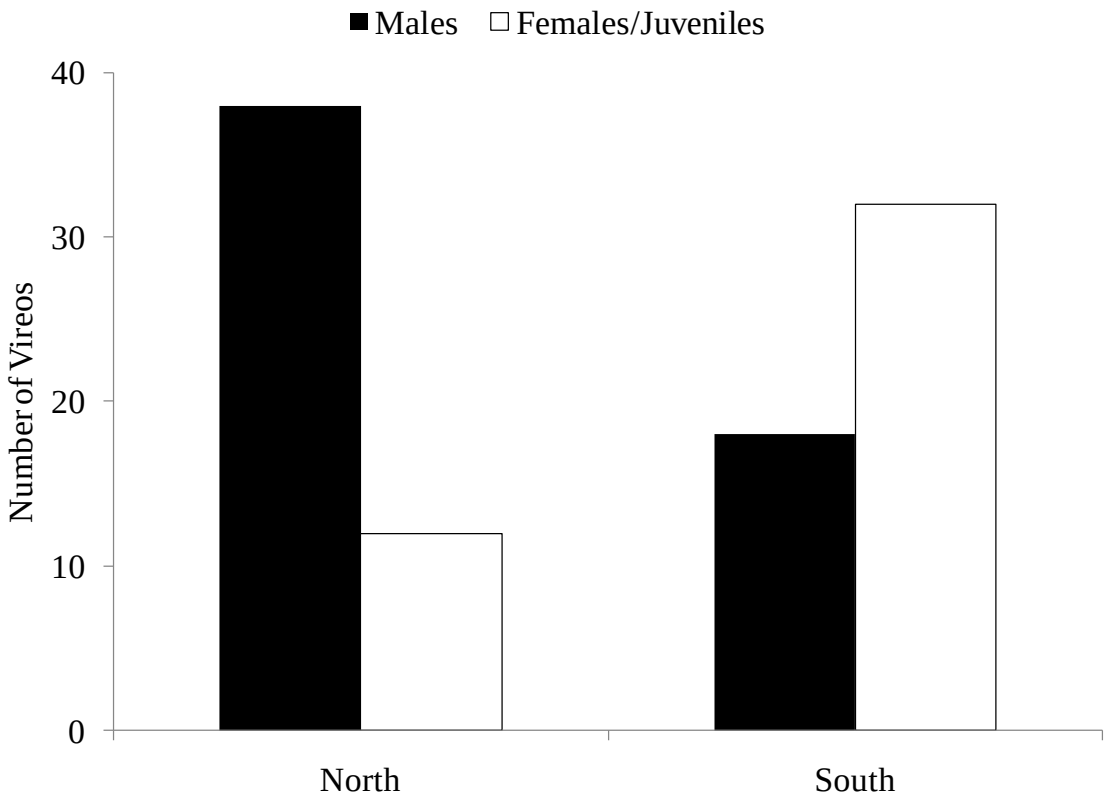

Figure 2.3. The number of black-capped vireos occupying habitats to the north and south of the median latitude of all wintering vireos in the nonbreeding winter range in western Mexico, 2003–2004, as a function of sex and age class.

Table 2.4. Contingency table for the Chi-square test of independence comparing observed and expected counts of adult male versus female and juvenile black-capped vireos in the northern and southern quartiles (the upper and lower 25% of records) of the wintering range at sites in western Mexico, 2003–2004. Expected counts are shown in parentheses. The Chi-square test showed an association between sex and winter latitude for black-capped vireos ($\chi^2 = 9.680$, df = 1, $P = 0.002$).

Sex/Age	North	South	Total
Adult Male	18	7	25
	(12.5)	(12.5)	
Female and Young	7	18	25
	(12.5)	(12.5)	
Total	25	25	50

Table 2.5. Analysis of winter-season latitudinal segregation by sex among 12 species of North American vireos based on museum specimen records. For each species, counts of sex are presented to the north and south of the median latitude of all individuals for that species. The χ^2 values and *P*-values were determined using a Chi-square test of independence. *P*-values < 0.05 are indicated by a double asterisk (**) and *P*-values < 0.10 are indicated by a single asterisk (*).

Species		*n*	Males north	Males south	Females north	Females south	χ^2	*P*
Black-capped vireo	*Vireo atricapilla*	28	11	6	3	8	3.743	0.053*
Bell's vireo	*V. bellii*	192	63	49	33	47	4.200	0.040**
Cassin's vireo	*V. cassinii*	34	10	7	7	10	1.059	0.303
Yellow-throated vireo	*V. flavifrons*	134	43	33	24	34	3.040	0.081*
Warbling vireo	*V. gilvus*	370	114	101	71	84	1.876	0.171
White-eyed vireo	*V. griseus*	568	182	166	102	118	1.899	0.168
Hutton's vireo	*V. huttoni*	410	128	129	77	76	0.010	0.919
Red-eyed vireo	*V. olivaceus*	426	150	133	63	80	3.042	0.081*
Philadelphia vireo	*V. philadelphicus*	100	31	32	19	18	0.043	0.836
Plumbeous vireo	*V. plumbeous*	34	16	11	1	6	4.497	0.034**
Blue-headed vireo	*V. solitarus*	120	33	25	27	35	2.136	0.144
Gray vireo	*V. vicinior*	22	6	3	5	8	1.692	0.193

Discussion

This is the first study of black-capped vireo winter occupancy that included survey efforts outside of Sinaloa and Nayarit and that covered most states within the potential winter range. The previously described non-breeding, winter range for the black-capped vireo extends southward from southern Sonora to Oaxaca and includes the states of Sonora, Sinaloa, Durango, Nayarit, Jalisco, Colima, Michoacán, Guerrero, and Oaxaca (Fig. 1.1). I documented black-capped vireo winter occupancy in Sinaloa, Durango, Nayarit, Jalisco, and Colima, but not in Sonora, Guerrero, Michoacán, or Oaxaca (Appendix A). No sites were surveyed in Sonora because it is unlikely to represent part of the normal winter distribution for the black-capped vireo, as described earlier. However, recent modeling efforts describing the potential winter distribution of the species includes Sonora (Vega Rivera et al. 2010), although current modeling efforts (Sarkar et al., unpublished) using a larger set of presence data (primarily my own) and a wider class of environmental variables have refined the potential distribution, which does not include any locations in Sonora, but does extend further south into Chiapas. Museum records include black-capped vireos from Michoacán (1) and Oaxaca (2), but none from Sonora and Guerrero.

The inability to locate any vireos in the southern states of Guerrero, Michoacán, and Oaxaca may result from several factors. It was more difficult to find adequate locations for surveying because economic development has been slower in these historically poor states, resulting in a less extensive road network extending inland from the coast relative to some other states. However, suitable habitat may be available

further inland in less accessible locations. The potential winter distribution for the black-capped vireo described by Vega Rivera et al. (2010) includes extensive inland areas within the southernmost states, and more recent modeling efforts (Sarkar et al., unpublished) indicate that Guerrero and Oaxaca may contain more black-capped vireo habitat than any other states.

Because Michoacán, Guerrero, and Oaxaca are further south and generally have poor roads, a history of regional conflict, and personal safety concerns, these states generally have been less visited by biologists, birders, and specimen collectors resulting in less information available from which to identify potential survey sites. Additionally, I generally did not have field assistance while in the southern states and visited these states toward the end of each winter. The combination of logistic constraints, time constraints, and reduced manpower resulted in lower search effort relative to other states. For example, only 15.2% of total search effort during this study was conducted in the states of Michoacán, Guerrero, and Oaxaca (Table 2.2).

Furthermore, it is possible that vireos were already migrating by the time I surveyed some of these locations. The first black-capped vireos can arrive in Texas as early as late March (Oberholser 1974), which approximates the time I began surveys in these southern states during the first two years of this study[1]. Thus, the inability to locate any black-capped vireos in Guerrero, Michoacán, or Oaxaca does not necessarily

[1] In 2001-2002, my first survey in Michoacan was on 17 March, my first survey in Guerrero was on 29 March, and my first survey in Oaxaca was on 6 April. In 2002-2003, my first survey in Guerrero was on 3 April and my first survey in Oaxaca was on 6 April. In 2003-2004, my first survey in Michoacan was on 26 February, my first survey in Guerrero was on 29 February, and my first survey in Oaxaca was on 10 March.

indicate they do not occupy those states during the winter. In fact, recent modeling efforts suggest occupancy is likely in all three of these southern states (Vega Rivera et al. 2010). Indeed, recent surveys for vireos in Michoacán, Guerrero, and Oaxaca located some individuals in all three states (M. Colon, unpublished data).

Nevertheless, most field evidence to date indicates that black-capped vireos do not occupy the southernmost states with the frequency they occupy some of the more northern states. Graber (1961) described Sinaloa and Nayarit as the center of the winter range for the black-capped vireo, and Gonzalez-Medina et al. (2009) also discussed the importance of Sinaloa to the species. Although both previous studies were conducted solely in the states they concluded were important, observations from this study also suggest the importance of Sinaloa and Nayarit for black-capped vireos. Of the 71 vireos documented during this study, 33 (46%) were in Nayarit and 17 (24%) were in Sinaloa. However, survey effort was not equal between states because it was largely dictated by opportunity and, as discussed above, survey opportunities were not equally distributed across states (Table 2.2). Among the 29 black-capped vireo museum records used in this analysis, 16 (55%) were collected from either Sinaloa or Nayarit, and only 3 (10%) were collected from the 3 southernmost states. However, this too may at least partially result from uneven survey effort across states, although the extent of this is unknown. Combined survey effort for Michoacán, Guerrero, and Oaxaca (364 hours; Table 2.2) was more than that for Colima (320), but I found 14 vireos in Colima and none in the southern three states, which provides some evidence suggesting their abundance is reduced in the southern states. Similarly, recent field investigations in Mexico found

more than twice as many vireos in the northern states as in the southern states despite similar survey effort across states (M. Colon, unpublished data).

The apparent higher occupancy of wintering black-capped vireos in the northern states relative to the southern states may reflect differences in habitat availability. Some of the largest tracts of remaining tropical dry forest in Mexico exist in Sinaloa (e.g., Trejo and Dirzo 2000, Cue-Bar et al. 2006, Rickers et al. 2007), which largely reflects the fact that conversion to agriculture, grazing, and other uses has been less intense in Sinaloa than in other states. Anthropogenic conversion of tropical dry forest (measured as percent loss) has been more intense in states such as Jalisco (67.2%), Michoacán (65.7%), Oaxaca (55.9%), and Guerrero (38.1%) than in Sinaloa (36.0%; Toledo and Ordonez 1993). Thus, relatively larger numbers of wintering black-capped vireos in Sinaloa may reflect availability of tropical dry forest.

Still, black-capped vireo habitat in Sinaloa is under heavy modification. It has been estimated that 50% of native vegetation in Sinaloa has been altered for human activities (primarily agriculture and cattle grazing), with thorn scrub and tropical semi-deciduous forest habitats being most heavily impacted (CONABIO 1999, Gonzalez-Medina et al. 2009, Leal-Sandoval et al. 2009). Modeling by Sarkar et al. (unpublished) estimates that a lower percentage of potential black-capped vireo habitat in Sinaloa is protected land than in some other states where I found vireos (i.e., 1.8% of land in Sinaloa vs. 14.7% in Nayarit, 12.7% in Jalisco, and 4.7% in Colima). Conversely, it is encouraging that the largest percentage of protected land among these states with known vireo use is Nayarit, the state in which I found more vireos than any other state.

Based on their distribution models, Vega Rivera et al. (2010) concluded that the black-capped vireo favored the lower elevation tropical dry forests and clearly avoided temperate areas at higher elevations. Specifically, 35% of the predicted winter distribution of the black-capped vireo is located at elevations of 0-500 m, 48% at elevations of 500-1250 m, and 17% at elevations above 1250 m in their study. Results from my study demonstrate patterns of elevation distributions similar to the predicted models of Vega Rivera et al. (2010). Locations of black-capped vireos in my study included 38% at elevations of 0-500 m, 54% at elevations of 500-1250 m, and 8% at elevations above 1250 m (Appendix A).

According to the best models of Vega Rivera et al. (2010), the predicted winter distribution of the black-capped vireo in Mexico covers an area of about 141,000 km^2. Recent models by Sarkar et al. (unpublished) refined the predicted winter distribution and produced a smaller estimated winter range of 103,000 km^2. Only 39.6% of this predicted area is in the states where I found all of the vireos in this study (i.e., 5.1% of the predicted distribution is in Sinaloa, 15.3% in Nayarit, 2.9% in Colima, 2.5% in Durango, and 12.8% in Jalisco; Sarkar et al. unpublished). The rest of the predicted distribution is in the southern states of Guerrero (29.7%), Oaxaca (16.5%), Michoacan (8.7%), and Chiapas (5.8%; Sarkar et al. unpublished). Considering that well over half of the predicted winter distribution occurs in the southern states where very few vireos have ever been detected by me or anybody else, more field research in these states should be considered a high priority.

This study provides evidence that differential migration occurs among wintering black-capped vireos, as demonstrated by latitudinal segregation among age and sex classes. I found a strong association between sex/age class and winter latitude (Table 2.3), an association that remained significant even under the more strict statistical comparison of latitudinal quartiles (Table 2.4). In both analyses, adult males occupied winter habitat at more northerly latitudes and females and juveniles occupied winter habitat at more southerly latitudes (Table 2.3, Fig. 2.3). Although these analyses did not differentiate between the effects of sex and age due to the difficulties of making such differentiation in the field, the analysis of museum specimen data revealed additional evidence of latitudinal segregation by sex for black-capped vireos (Table 2.5).

Three primary hypotheses describe the non-random distribution of age and sex classes over a latitudinal gradient during winter (reviewed by Myers 1981, Ketterson and Nolan 1983, Cristol et al. 1999). The *arrival-time hypothesis* predicts that adult males select more northerly winter sites to allow for earlier spring arrival and establishment of high-quality territories on the breeding grounds, thus increasing their likelihood of successful breeding (King et al. 1965, Ketterson and Nolan 1976, Myers 1981). When male birds show intrasexual competition for territories and greater site fidelity to breeding sites than females, selection should favor early arrival by adult males, and thus differential winter distribution should occur (Ketterson and Nolan 1983). This may be the case for black-capped vireos, because male vireos arrive on the breeding grounds first, compete for territories, and show greater site fidelity than females (Graber 1961, Grzybowski 1995).

Alternatively, the *dominance hypothesis* states that geographic segregation may result when dominant individuals force socially subordinate individuals to migrate farther away from the breeding grounds in the nonbreeding season to reduce competition (Gauthreaux 1978, 1982). Lack (1954) proposed that the dominant sex (males) can exclude others from certain areas, an idea that could be extended to include differences in geographic wintering areas (Selander 1966, Lynch et al. 1985, Morton 1990). Thus, if adult males are dominant to female and young black-capped vireos, then the dominance hypothesis may explain the observed latitudinal segregation.

For birds wintering in temperate areas (e.g., short-distance migrants or winter residents), the *body-size hypothesis* states that, relative to smaller individuals, larger individuals (usually males and adults) can physiologically withstand the colder environments of higher latitudes, and thus winter at higher latitudes (Ketterson and Nolan 1976, 1979). The smaller surface area to body-volume ratio and lower mass-specific metabolic rate of larger individuals enhance tolerance to cold temperatures and periods of food shortage (Kendeigh 1945, Calder 1974). Because this hypothesis only applies to birds where cold weather is a constraint (e.g., short-distance migrants wintering in temperate climates), it is not a viable explanation for the observed patterns among black-capped vireos.

In a review of published studies on differential migration, Cristol et al. (1999) found support for each of these hypotheses, but the relationship between migration distance and the explanatory variables (i.e., body size, dominance, and arrival time) is confounded by covariation between each independent variable and age or sex, because

both age and sex are also related to migration distance. Additionally, the hypotheses are not mutually exclusive, and in many species, adult males are the largest individuals, are socially dominant, and return to breeding areas first, making it difficult to assess which mechanism is responsible for differential migration.

In addition to the role of environmental influences (e.g., competition for food or nest sites) on differential migration, the behavioral basis of latitudinal sexual segregation also may be developmentally fixed and controlled by endogenous circannual rhythms (Holberton 1993, Terrill and Berthold 1989). For example, in a laboratory investigation of dark-eyed juncos (*Junco hyemalis*), females exhibited a longer migration period (i.e., they began to show migratory activity significantly earlier than males and ceased activity later than males), suggesting females of this species migrate further than males (Holberton 1993).

Differences in the onset of fall migration may result from differential timing of molt between the sexes (Chandler and Mulvihill 1990, Holberton 1993, Coppack and Pulido 2009). Young and female black-capped vireos begin fall migration prior to adult males (Graber 1961, Marshall et al. 1985). Prior to fall migration, male vireos begin prebasic molt earlier than females but both sexes complete molt at similar times, indicating that females molt more rapidly (L. Butler, unpublished data). The more rapid molt of feathers by females may reduce feather quality because faster molting leads to shorter, lighter, less symmetrical feathers with less rigid, less stiff, and thinner rachises and consisting of softer keratin (Dawson et al. 2000, de la Hera et al. 2010). Lower feather quality may reduce flight performance, increase thermoregulatory costs, and

reduce winter survival (Nilsson and Svensson 1996, Swaddle et al. 1996, Dawson et al. 2000, de la Hera et al. 2010). Reduced female winter survival resulting from more rapid feather molt and from longer migration distances (i.e., because they occupy more southerly winter habitats) may be factors contributing to the general pattern of male-biased sex ratios observed on the breeding grounds for black-capped vireos (e.g., Tazik 1991, Grzybowski 1995).

Skewed adult sex ratios also are known to result from latitudinal segregation (Komar et al. 2005). In a review of 201 published estimates of avian adult sex ratios, Donald (2007) found skewed adult sex ratio's for 65% of species studied, with a mean ratio of 0.56, demonstrating a skew toward more males. Given that offspring sex ratios are generally balanced, higher mortality of the rarer sex is the only explanation for skewed sex ratios among adult birds (Donald 2007). Survival rates of adult female birds appear to be systematically lower than those of males (e.g., Promislow et al. 1992, Liker and Szekely 2005, Donald 2007), and several studies have empirically demonstrated lower survival of the rarer sex (usually the female) as the cause of skew in avian adult sex ratio (see Szekely et al. 2006 and Donald 2007). Threatened species showed a significantly more male-skewed adult sex ratio than non-threatened species, and there was a tendency for the skew toward males to increase with increasing threat status (Donald 2007).

Theoretical models predict that in monogamous mating systems, extinction probability is likely lowest when the sex ratio is balanced (Bessa-Gomes et al. 2004). Extinction risk is predicted to increase more rapidly with increasingly male-skewed adult

sex ratios and population viability analyses predict a decline in viability once the adult sex ratio exceeds 0.55 (Morales et al. 2005). Heavily skewed adult sex ratios may pose further threats to small populations, and a skewed adult sex ratio may explain higher levels of sexual selection in threatened than in non-threatened bird species (Morrow and Pitcher 2003, Donald 2007).

Research on adult sex ratios in black-capped vireos is limited, but there is some evidence that adult sex ratios may approximate the 0.55 cutoff above which population viability may decline. For example, Grzybowski (1995) reports adult sex ratios from his own research of 0.61 and 0.53 for different populations, and also cites work from Tazik (1991) reporting an adult sex ratio of 0.51, while Graber (1961) documented adult sex ratios of 0.53, producing an overall average (among the 4 cited values) of 0.55. The limited data available at least suggests that skewed sex ratios may be important, although further investigation of sex ratios among black-capped vireos is needed.

The mechanism underlying differential survival between the sexes most likely relates to physiological, ecological, genetic, and behavioral differences (Donald 2007). In most bird species, including the black-capped vireo (Athrey et al. 2012), females disperse more than males, exposing them to greater risk and increased mortality (Martin and Li 1992, Donald 2007). Also, intersexual differences in foraging behavior and energy demands during the breeding season are known to occur, leading to higher mortality in one sex (e.g., Lewis et al. 2002, Phillips et al. 2004, Post and Gotmark 2006), and these differences may reflect dominant males competitively excluding smaller females from better habitats (Benkman 1997, Marra and Holmes 2001, Pechacek

2006). Breitwisch (1989) and Liker and Szekely (2005) suggested that events during the nonbreeding period primarily are responsible for higher female mortality in bird populations with skewed adult sex ratios. Among migratory species that engage in differential migration, females may experience greater mortality risks from longer flights (Stouffer and Dwyer 2003, Catry et al. 2005). Also, differences in winter habitat quality for classes of populations that segregate on the wintering grounds may influence adult sex ratios as well (Woolfenden et al. 2001, Donald 2007).

The present study found female black-capped vireos wintering at more southerly latitudes than males. The longer migration by females than males may result in higher mortality rates among females. Evidence of sex-specific differences in survival among black-capped vireos comes from a male-skewed adult sex ratio (Tazik 1991, Grzybowski 1995) and from male-biased differences in return rates to the breeding grounds (e.g., Graber 1961, Tazik and Cornelius 1993). Furthermore, Promislow et al. (1992) reported annual mortality of 0.298 for male black-capped vireos versus 0.593 for females, calculated from data in Graber (1961). However, Kostecke and Cimprich (2008) documented lower recapture probabilities of females, which they suggested may bias estimates of sex-specific differences in survival.

Another predictor of adult sex ratios relates to arrival time for long-distance migrants (Rubolini et al. 2004, Kokko et al. 2006, Donald et al. 2007). Protandry, the earlier arrival of males relative to conspecific females at the breeding grounds, is a common pattern of sex-biased timing for many migratory species (Myers 1981, Gauthreaux 1982, Ketterson and Nolan 1983, Francis and Cooke 1986, Morbey and

Ydenberg 2001). Protandry occurs among black-capped vireos, with adult males typically arriving 1-2 weeks before females and first-year males (Graber 1961). Recent evidence that male-biased adult sex ratios may be associated with, and even cause, protandry in birds comes from models backed by field investigations (Kokko et al. 2006, Amrhein et al. 2007).

Morbey and Ydenberg (2001) reviewed and classified seven hypotheses for protandry in wildlife populations, two of which are of particular relevance among avian studies: the *rank advantage hypothesis* and the *mate opportunity hypothesis*. The rank advantage hypothesis states that competition for high-quality territories selects for the earliest arriving males (Ketterson and Nolan 1976, Myers 1981, Kokko 1999). This hypothesis has garnered the most attention among avian studies because the territorial sex generally arrives earlier than the non-territorial sex in birds (e.g., Myers 1981, Francis and Cooke 1986, Morbey and Ydenburg 2001), which is the case for the black-capped vireo (Graber 1961).

Alternatively, according to the mate opportunity hypothesis, competition for mates, rather than male-male competition for territories, determines the degree of protandry, which may allow polygynous males to maximize their opportunities (reduced sperm competition and increased opportunity for extra-pair copulations) to mate with females (Hasselquist 1998, Rubolini et al. 2004, Coppack et al. 2006, Kokko et al. 2006). Support for the mate opportunity hypothesis comes from experimental research (Hasselquist 1998) and studies showing positive associations between protandry and indicators of the intensity of sexual selection through female choice, such as sexual

dichromatism (Rubolini et al. 2004), sexual size dimorphism (Kissner et al. 2003), and the rate of extra-pair paternity (Coppack et al. 2006). Morbey and Ydenberg (2001) suggest that the rank advantage and mate opportunity hypotheses may operate together if high-quality territories help in acquiring more mates.

A third hypothesis for protandry, the *constraint hypothesis*, may be important for species that exhibit differential migration. The constraint hypothesis states that selection may act indirectly on arrival timing through selection on a trait other than arrival timing (Gauthreaux 1978). For example, if selection results in male birds spending the winter farther north than females, but both sexes migrate at the same time and same rate, then males will arrive at the breeding areas sooner than females. As with the hypotheses for differential migration, it is unclear which of the proposed hypotheses ultimately explains the earlier arrival of male black-capped vireos on the breeding grounds, and this is an area where more research is needed.

While many studies have examined the ultimate (evolutionary) causes of protandry (discussed above and reviewed in Morbey and Ydenberg 2001), few studies have looked at the proximate (mechanistic) causes (Coppack et al. 2006, Coppack and Pulido 2009). Sexual differences in time of arrival may be caused by three, not mutually exclusive, mechanisms: 1) males may migrate faster than females by requiring less time for stopover; 2) males may travel shorter distances by wintering closer to the breeding grounds than females; and 3) males may initiate spring migration earlier than do females (Coppack and Pulido 2009). Among passerine birds, most evidence suggests that latitudinal segregation during the nonbreeding period and differences in the initiation of

spring migration are the primary determinants of protandrous arrival at breeding sites (Coppack and Pulido 2009). Thus, the pattern of latitudinal segregation among black-capped vireos described in this study may explain the earlier arrival of male vireos to the breeding grounds relative to females. Alternatively, timing of spring migration may be an important factor, but we do not know if male black-capped vireos initiate spring migration earlier than females.

Evidence from several species indicates that sex-specific differences in the onset of migration may result from different endogenous cycles or photoperiodic sensitivities (e.g., Ketterson and Nolan 1985, Terrill and Berthold 1990, Berthold 2001, Coppack and Pulido 2009). Additionally, physical condition or physiological state may modify the timing of migration in spring. For example, the effect of winter habitat quality on physical condition is known to influence the timing of migration (e.g., Marra and Holmes 2001, Bearhop et al. 2004, Norris et al. 2004, Saino et al. 2004, Studds and Marra 2005). As an extension of the dominance hypothesis, dominance behavior by certain classes of individuals also may influence body condition and survival. For example, dominant individuals (e.g., adult males) have greater access to limited habitats and food resources throughout the nonbreeding season and consequently are better able to gain body weight and reduce winter mortality (Gauthreaux 1978, 1982; Ketterson and Nolan 1979, Lundberg 1985).

Individuals that spend the nonbreeding season in high-quality habitats are in better physical condition and are better able to accumulate fat deposits needed for migration, allowing them to depart the winter grounds earlier than birds wintering in

sub-optimal habitats. For example, sexual segregation of American redstarts (*Setophaga ruticilla*) among habitat types on their Jamaican wintering grounds leads to differences in food quality and availability, which results in differences between the sexes in survival, body condition, and ultimately, date of departure (Marra et al. 1998, Marra and Holmes 2001).

In the present study, body condition (i.e., fat score) was generally higher for adult male vireos relative to female and young birds, although the difference was not statistically significant. It is possible these results are somewhat confounded by the combination of females with young males, and that the difference in body condition between males and females is more significant. If male black-capped vireos are in better body condition than females, this may partially explain the earlier arrival of males on the breeding grounds as well as the lower survival of females as evident in the male-skewed sex ratios. Additionally, differences in body condition may allow adult males to migrate earlier than females and young during the spring, which (in addition to latitudinal segregation) would explain the pattern of protandrous arrival of adult male vireos to the breeding grounds (e.g., Graber 1961).

Another potential implication of a skewed sex ratio relates to mating system and its influence on avian populations. Avian mating systems may not only be flexible, but dictated by the adult sex ratio (Donald 2007), and mating system may influence the effective population size in populations with skewed sex ratios (Nomura 2002). Variation in adult sex ratio may increase mate-guarding behavior by males (Major 1992) and result in a population of non-breeding male floaters (Githiru et al. 2006). Flexibility

in mating systems may buffer populations from the increased extinction risk associated with skewed adult sex ratios (Rossmanith et al. 2006), and much of the variation in mating systems observed in birds may be a simple response to variation in adult sex ratio caused by other factors (Donald 2007). For example, a male-skewed adult sex ratio may promote monogamy and male-male competition because a single female would be of great value to a male in a system where females are relatively rare (Ligon 1999). Thus, intense sexual selection, such as dichromatism, may result from skewed adult sex ratios. Therefore, adult sex ratio may provide an important metric regarding the intensity of sexual selection (Emlen and Oring 1977, Kvarnemo and Ahnesjo 1996, Wiegmann and Nguyen 2006).

The mating system for black-capped vireos is somewhat flexible, as pairs may be monogamous, sequentially polygynous (males), or sequentially polyandrous (females) within a breeding season (Grzybowski 1995). Black-capped vireos also may engage in extra-pair copulation, but this area needs more research (Grzybowski 1995). The flexibility of the vireo mating system may be a response to variations in adult sex ratios that may serve to reduce extinction risk for local populations. Additionally, sexual dichromatism among black-capped vireos may be a sexually selected response to a male-biased adult sex ratio.

The degree of protandry exhibited by bird species is positively associated with sexual dichromatism because of the relationship of the latter to sperm competition (Rubolini et al. 2004). Promislow et al. (1992) showed that sexual dichromatism among passerines was associated with higher mortality rates, leading to the prediction that

extinction rates should be higher for populations/species with intense sexual selection. Doherty et al. (2003) tested this prediction by analyzing the dynamics of bird communities over a 21-year period, and found that dichromatic species had significantly higher chances of becoming locally extinct compared with monochromatic species. Support for this prediction also comes from independent tests of the fate of bird species introduced to oceanic islands, where dichromatic species were more likely to go locally extinct compared to monochromatic species (McLain et al. 1995, Sorci et al. 1998). Potential explanations for why sexually selected species are more prone to local extinction include increased risks of predation (Endler 1980, 1983) and parasitism (Sheldon and Verhulst 1996, Verhulst et al. 1999), reduced effective population size because of reproductive skew (Waite and Parker 1997), and antagonistic coevolution between the sexes (Holland and Rice 1999).

Doherty et al. (2003) also showed that local species turnover rate was higher for dichromatic species than monochromatic species, suggesting that dispersal between sites, allowing high turnover, may be critical for population persistence in dichromatic species. Thus, dichromatic species may depend more heavily than other species on dispersal and recolonization for local dynamics, and these species may be more susceptible to environmental changes that limit dispersal effectiveness (Doherty et al. 2003).

The black-capped vireo may not be effectively dispersing and recolonizing sites, however, and genetic differentiation still exists between many sites even where habitat is abundant, such as in central Texas (Barr et al. 2008, Athrey et al. 2012, but also see Zink

et al. 2010). Sexually selected species also may be more vulnerable to habitat degradation because sustained sexual selection on males may compromise their adaptation with respect to other components of fitness (McLain 1993, McLain et al. 1995). It is unclear if black-capped vireos are more susceptible to habitat degradation and environmental change than other species, but this should merit more attention because of its management and conservation implications.

Sexual dichromatism also may increase the variance in male fertilization success as female choice for brighter males increases levels of extra-pair copulations (Moller and Birkhead 1994). This skew in male reproductive success may reduce the effective population size and increase extinction risk for dichromatic species (Foose et al. 1995, Sorci et al. 1998). Webster and Marra (2005) suggested that seasonal interactions play an important role in driving rates of extra-pair copulation by influencing the timing of female migration and the physical condition of females upon arrival at the breeding grounds. For example, females from poor quality winter habitats may be more likely to engage in extra-pair copulation because if poor body condition on the wintering grounds delays spring departure, their subsequent late arrival on the breeding grounds makes it more difficult to find unpaired high-quality males (Webster and Marra 2005). Dimorphic species exhibiting high levels of extra-pair paternity also experience higher levels of nestling mortality through nest predation (Moller and Birkhead 1994, Weatherhead et al. 1994).

It is unknown if survival rate is lower in the sexually dimorphic black-capped vireo than in monomorphic vireo species, or if black-capped vireos more frequently

engage in extra-pair paternity or experience higher levels of nest predation, but evidence from other species suggests these patterns may be possible. Because of the reduced survival and potential for higher nest predation rates faced by sexually selected (e.g., dichromatic) species, they may be more vulnerable to environmental stochasticity than species that are not sexually selected (Sorci et al. 1998). Support for these views comes from evidence that extinct or endangered species are more often dichromatic than other species within the same families (Sorci et al. 1998).

My prediction that black-capped vireo would be the only species to show patterns of latitudinal sexual segregation among 12 species of migratory North American vireos was not supported by the analysis of museum specimen records. I found an association between sex and winter latitude for black-capped vireo, Bell's vireo, plumbeous vireo, red-eyed vireo, and yellow-throated vireo (Table 2.5), although I am cautious in including plumbeous vireo because of low sample sizes.

Although these results seem inconsistent with the expected relationship between dichromatism and sexual segregation, it may be more consistent than at first thought. Traditionally, scientists have considered a species dichromatic when there is an apparent color difference between males and females (e.g., Sorci et al. 1998, Badyaev and Hill 2000, Dunn et al. 2001, Badyaev and Hill 2003), but the validity of this approach depends on the ability of humans to visually assess avian coloration. Recent research, however, has demonstrated that ultraviolet (UV) vision may be an important aspect of mate choice in birds (Bennett et al. 1994), and therefore human perception of dichromatism may not reflect the actual color patterns that birds can use to discriminate

potential mates. Unlike humans, many birds see UV wavelengths due to the presence of a fourth cone cell type in the avian retina that is receptive to UV light (Cuthill et al. 2000, Odeen and Hastaad 2003), indicating that previous interpretations of avian plumage coloration may be misleading (Cuthill et al. 1999).

Thus, many species that appear sexually monochromatic to humans may in fact be sexually dichromatic from an avian visual perspective (Eaton 2005). Indeed, Eaton (2007) demonstrated that the vast majority of passerines considered sexually monochromatic by humans were sexually dichromatic from an avian visual perspective, including 9 species of vireos (blue-headed, Bell's, gray, Hutton's, Philadelphia, red-eyed, white-eyed, and yellow-throated; the author found warbling vireo to be monochromatic and did not evaluate black-capped, Cassin's, or plumbeous vireos). However, Eaton (2007) evaluated dichromatism across several feather patches (i.e., head, chest, throat, back, belly, tail, scaps), and some species exhibited dichromatism consistently across different feather patches whereas others did so for only one or two feather patches. Among the vireos, consistent evidence of dichromatism across several feather patches was exhibited by Bell's, red-eyed, white-eyed, and yellow-throated vireos (Eaton 2007). Thus, the species showing the strongest patterns of dichromatism included 3 (Bell's, red-eyed, and yellow-throated) of the 4 species of vireos for which I found an association between sex and winter latitude, the fourth being the black-capped vireo that we already know is sexually dichromatic. Among vireo species known to be sexually dichromatic, the evidence seems to support the predicted relationship between

dichromatism and sexual segregation, although more research on this relationship is needed.

Sexual dichromatism in black-capped vireos may indicate some potential conservation problems for the species. Sexual dichromatism is thought to have evolved in response to selection pressures that differ between the sexes, whereby variation in plumage coloration can be used by conspecifics to gather information about an individual's quality as a potential mate or competitor (Andersson 1994, Badyaev and Hill 2003). Females may prefer the most extravagantly ornamented males because they are sexually more attractive (Fisher 1930), more resistant to parasites and pathogens (Hamilton and Zuk 1982), less profitable to predators (Baker and Parker 1979), or better parents (Heywood 1989, Hoelzer 1989). However, the evolution of exaggerated ornamentation and coloration that promote male reproductive success also may exert viability costs that reduce survival (Lande 1980, Kirkpatrick 1982, Moller and de Lope 1994). Sex-biased mortality is positively correlated with male plumage brightness in birds (Promislow et al. 1992, 1994) and brightly colored birds may attract predators more than do inconspicuous species, which can represent an additional source of mortality for both adults and nestlings (Barber 1993, Haskell 1996).

If the sexes differ in the timing and extent of migration, males and females may be exposed to different environmental conditions since they may use different habitats during winter and may experience different climatic conditions during migration (Rainio et al. 2007, Coppack and Pulido 2009). Changes in migration phenology (e.g., resulting from climate change) are likely to affect timing of the initiation of breeding, and changes

in the timing of arrival to breeding areas may affect the sexes differently in species with sex-differentiated migration strategies (Tottrup and Thorup 2008). Therefore, relative differences in the influence of changing ecological conditions on males and females may affect mating decisions, reproductive success, and population viability (Morbey and Ydenberg 2001).

Another possible result of a warming climate is that warming spring temperatures may increase pre-breeding survival rates and lead to even earlier spring arrival of males competing for territories (Moller 2004, 2007; Spottiswoode et al. 2006), which may increase the time lag between the arrival of males and females, as has been shown already in some species (Moller 2004, Moller and Szep 2005). However, the ability of species, such as the black-capped vireo, that winter in western Mexico to advance the timing of spring departure may be constrained in the future by conditions on the winter grounds. Departure dates by migratory birds depend upon pre-migratory fueling on arthropods, which itself depends upon patterns of rainfall (Brown and Sherry 2006a, Studds and Marra 2007, 2011). Climate models project a decreasing pattern of precipitation across western Mexico (IPCC 2001, Gomez-Mendoza and Arriaga 2007, Saenz-Romero et al. 2010), which suggests there will be delays in the timing of spring departure for migratory songbirds at the very time when the adaptive response to changing conditions on the breeding grounds would be selection for advancing spring departure dates (Studds and Marra 2007). If inadequate pre-migratory food conditions limit the ability of the black-capped vireo to advance its spring departure timing, its individual fitness, reproductive success, and population viability may be diminished.

Adaptive constraints on migratory birds during one period may compromise adaptive solutions for another (Mills 2005). Many migratory birds that are habitat-specific in the breeding period may exhibit reduced habitat specificity during other periods of the annual cycle (Mills 2005). They may be less habitat-specific during migration (Wang and Finch 2002), and although some migrant passerines are habitat-specific during winter (Murphy et al. 2001), others occupy diverse habitats during this period (e.g., Wunderle and Waite 1993, Latta and Faaborg 2002). Mills (2005) argues that it may be a necessity for most migratory passerines to demonstrate flexibility in exploiting different habitats considering the multitude of environments migrants experience over the annual period. Strongly sexually selected species may be more vulnerable to extinction under conditions of environmental change (e.g., climate change) than other species because strong sexual selection pressures (i.e., the evolved allocation of energy to mate acquisition) may be so high that insufficient energy is available for acclimation to new ecological demands or natural selection pressures (McLain 1993, McLain et al. 1995).

Among temperate-breeding North American passerines, males in some species stay conspicuous during the nonbreeding season while males in other species become dull. Male black-capped vireos remain conspicuous, even though they are somewhat duller than during the breeding season (Pyle 1997, Froehlich et al. 2005). The *molt constraints hypothesis* predicts species that remain conspicuous in the winter season do so because they cannot afford a complete (prealternate) molt of body feathers in spring, implying that conspicuous winter plumage may be maladaptive (Froehlich et al. 2005).

More recent research also indicates that sexual dichromatism among migratory species is maladaptive (Friedman et al. 2009). Seasonal color change could incur high energetic costs, especially if the spring molt coincides with a time of energetic stress arising from late-winter food limitation or conflicting requirements (Rohwer et al. 1983, Rohwer and Butcher 1988, Froehlich et al. 2005). Protein demands are high during molt, so insectivores may replace feathers more easily than may birds dependent on plant products, but the widespread dry season in the northern Neotropics is most severe between January and April, which is the spring molting period but also a time when arthropod levels are significantly depressed (e.g., Parrish and Sherry 1994, Strong and Sherry 2000, Latta and Faaborg 2001, Studds et al. 2011). Several species show associated effects on diet (Morton 1980), body condition (Strong and Sherry 2000, Marra and Holmes 2001), and seasonal distribution and spacing behavior (Parrish and Sherry 1994, Latta and Faaborg 2001). Thus, insectivores may be more likely to experience spring molt constraints (Froehlich et al. 2005).

Consistent with molt constraints, most sexually dichromatic songbirds of North America that undertake extensive spring molt do not have conspicuous winter coloration in males (Froehlich et al. 2005). Black-capped vireos have conspicuous male winter plumage and a partial spring molt (i.e., not entire body plumage) that includes all the dichromatic parts of the plumage, such as the head (Pyle 1997). Partial molts are unlikely to represent significant energetic costs (Pyle 1997, Froehlich et al. 2005). Most dichromatic taxa with dramatic seasonal color change (i.e., dull winter plumage) show extensive spring molts, whereas those with conspicuous winter plumage (e.g., black-

capped vireo) typically show no or partial spring body molts. This is likely a response to limited food availability during spring molt because it coincides with the dry season.

Dietary flexibility on the winter grounds (e.g., eating plant materials) may be critical for overcoming resource-based spring molt constraints faced by long-distance Neotropical migrants (Froehlich et al. 2005). Black-capped vireos appear to demonstrate some flexibility in their winter diet. Although vireos primarily consume insects during winter, I observed limited consumption of fruits (personal observation) during this study. Additionally, limited stomach content analyses of wintering vireos (n=3) documented consumption of vegetable matter as well (Graber 1961), with vegetable matter (seeds) comprising at least 50% of the stomach contents for two vireos versus less than 5% for all stomach samples from the breeding grounds (n=8). The possibility that black-capped vireos expand their diet in winter to molt dichromatic feathers indicates the importance of sexual selection in the life history of the species, although there is a clear need for a more intensive analysis of the winter vireo diet.

CHAPTER III

HABITAT USE OF BLACK-CAPPED VIREOS IN THE WINTER RANGE

Synopsis

Although the endangered black-capped vireo spends over half its annual life cycle either in migratory transit or on its non-breeding (winter) grounds in Mexico, little is known about this period of the species' life cycle. Because of the dearth of information about winter habitat use by black-capped vireos in Mexico, I initiated a study to 1) describe habitat characteristics of patches used by vireos during the winter; 2) determine which habitat characteristics may influence vireo use of winter patches; and 3) evaluate differences in habitat characteristics between patches across different latitudes, elevations, habitat types, and age/sex classes. Field research was conducted from 2003–2004 at study sites located along the Pacific lowlands of western and southern Mexico. Winter habitat use by black-capped vireos was best predicted by increasing values of slope and foliage cover, and by decreasing values of canopy cover and tree diameter. Vireo use plots characterized as thorn forest had greater foliage density, greater shrub density, less canopy cover, and smaller tree diameter than plots classified as tropical deciduous or semi-deciduous forest. Results from this study indicate thorn forests may be most suitable for vireo occupancy during the winter months. Deforestation is a major threat to the tropical dry forests in western Mexico, especially for thorn forests, which are more prone to conversion to agriculture. Ultimately, the long-term persistence of

black-capped vireos in their winter range may largely depend upon the conservation of these forests.

Introduction

Events or conditions in different stages of the annual life cycle of a bird can influence subsequent events for both the individual and the population. Individual birds carry over effects between seasons, such as physical condition or date of arrival, which can explain variation in reproductive success and annual survival (Fretwell 1972, Gill et al. 2001). For example, winter habitat quality and food availability directly affect body condition (Strong and Sherry 2000), which can indirectly affect reproductive success (Marra et al. 1998) and survival (Peach et al. 1991, Sillett et al. 2000). Winter habitat quality can influence timing of spring migration (Marra et al. 1998, Rockwell et al. 2012), which is important because individual migrants arriving early in temperate breeding areas may have higher reproductive success than those arriving later (e.g., Lozano et al. 1996, Hasselquist 1998, Harrison et al. 2011, Rockwell et al. 2012). Therefore, learning about habitat conditions for migratory birds during the nonbreeding season may help researchers and managers better answer questions about population-level differences observed on the breeding grounds.

It is thus important for biologists to identify which habitat attributes are used or selected by species of interest relative to the availability of those attributes. If animals select habitat features disproportionate to their availability, those features may improve their fitness or survival (Manly et al. 2002, Thomas and Taylor 2006, McLoughlin et al.

2010). Habitat use refers to the way individual organisms or species utilize habitats to meet their life history needs (Block and Brennan 1993), and habitat use patterns are the end result of habitat selection processes (Jones 2001). Habitat selection refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats or habitat attributes to influence survival and fitness of individuals (Hilden 1965, Cody 1981, Hutto 1985, Block and Brennan 1993, Mayor et al. 2009). The hierarchical organization of habitat selection includes selection of the geographic range of a species, within which individuals select specific home ranges, from which they use various habitat components (i.e., microhabitat) and select particular elements (e.g., food items) from those available at the site (Johnson 1980).

Habitat selection is often studied at the microhabitat level, focused on uncovering specific within-habitat attributes important to the study species. The study of habitat at the microhabitat level may be useful because many species respond to specific vegetation structures or abiotic conditions rather than broader components of the macrohabitat (Hilden 1965, Dueser and Shugart 1978, Morrison et al. 1992, McClure et al. 2012). Because vegetation structure is often highly variable within a plant association, habitat quality also varies greatly, making it important to identify the vegetation structure associated with habitat selection to effectively understand the microhabitat for any species of interest (North and Reynolds 1996).

The black-capped vireo is a small, migratory songbird with a current known breeding range including isolated portions of Oklahoma, central and southwestern Texas, and northeastern Mexico (Wilkins et al. 2006). The species arrives on territories

in Texas from mid-March to mid-April and in Oklahoma approximately 10 days later (Campbell 1995, Grzybowski 1995), and depart the breeding grounds in late August and September (Graber 1961, Marshall et al. 1985).

In 1987, the black-capped vireo was federally listed as an endangered species under the ESA of 1973 (Ratzlaff 1987). The primary threats to the species identified at the time of listing included habitat loss from development, nest parasitism by brown-headed cowbirds, and habitat destruction from the grazing of sheep, goats and exotic livestock (Ratzlaff 1987). All of the major threats described for the species pertained to the breeding grounds, and the species has generally received considerable attention in its breeding range (e.g., Graber 1961, Marshall et al. 1985, U.S. Fish and Wildlife Service 1991, Grzybowski 1995, Wilkins et al. 2006).

Nevertheless, individuals of this species spend over half their annual life cycle either in migratory transit or on their non-breeding (winter) grounds and little is known about these periods of the black-capped vireo's life cycle (Grzybowski 1995, Wilkins et al. 2006). The species may be vulnerable during the non-breeding period, and thus, learning more about ecology of this species during the non-breeding season is cited as one of the top research priorities in both the Black-capped Vireo Recovery Plan (U.S. Fish and Wildlife Service 1991) and the Black-capped Vireo Population and Habitat Viability Assessment Report (U.S. Fish and Wildlife Service 1996).

Most accounts of black-capped vireo winter distribution occur within the vegetation zone known as tropical dry forest, and include the Mexican states of Sinaloa, Durango, Nayarit, Jalisco, Colima, Guerrero, Michoacán, and Oaxaca. Tropical dry

forests are among the richest ecosystems in Mexico, a biologically rich country with approximately 10% of the world's organisms (Mittermeier 1988, Mittermeier et al. 1997, Groombridge and Jenkins 2000). Mexican dry forests maintain the highest levels of vertebrate endemicity of all Neotropical dry forests (Redford et al. 1990, Ceballos and Garcia 1995), harboring numbers of endemic vertebrate species comparable to those of cloud and conifer forests (Ceballos and Navarro 1991, Escalante et al. 1993). Mexico's tropical dry forests also harbor high floristic diversity (Lott et al. 1987, Gentry 1988, 1995, Trejo and Dirzo 2002) and floristic endemicity (Cue-Bar et al. 2006), containing nearly 40% of Mexico's endemic species and 20% of its total flora (Rzedowski 1991a, b).

The largest remaining Neotropical dry tropical forests north of the Equator are found in western Mexico (Ceballos and Garcia 1995). The Pacific coastal states of Sinaloa, Jalisco, Michoacán, Guerrero and Oaxaca rank among the 6 states with the largest total area (in declining order) of tropical dry forests in Mexico (Cue-Bar et al. 2006). Similarly, Trejo and Dirzo (2000) found significant masses of tropical dry forest in the lowlands of Sinaloa, western Jalisco, and the Balsas river basin along the border of Guerrero and Michoacán states, and Rickers et al. (2007) found some of the highest forest cover in Sinaloa and Durango states. Tree species richness in tropical dry forests is also generally highest in the states along the Pacific coast of Mexico. The Pacific coastal states of Guerrero, Jalisco, Oaxaca, Michoacán, Colima, Sinaloa, and Nayarit rank among the 8 states with the highest tree species richness (Cue-Bar et al. 2006). One reason for the high floral diversity and endemism is that the rugged topographic features

of the region promote a large beta-diversity (i.e., high turnover of species) through geographic isolation and local diversification (Gentry 1988, Rzedowski 1991a, Givnish 1999, Trejo and Dirzo 2002). The processes of fragmentation and expansion of tropical dry forests during and before the Pleistocene also may have driven plant speciation (Pennington et al. 2000, 2004).

Portions of the black-capped vireo's winter range have been investigated to a limited extent, although most of this information is anecdotal. Graber (1957, 1961) qualitatively assessed habitat characteristics at sites used by black-capped vireos in Sinaloa and Nayarit over a short period in December, 1955. She determined that black-capped vireos use a wider range of vegetation types on the winter grounds than they do on the breeding grounds, using both arid scrub and more mesic, luxuriant forest. However, Marshall et al. (1985) only found vireos in the more arid thorn forests during fieldwork conducted between September and November 1984, also restricted to Sinaloa and Nayarit. On the other hand, Gonzalez-Medina et al. (2009) found no black-capped vireos in thorn forest in a study restricted to Sinaloa, and most of the individuals they found were in tropical deciduous forests, especially when in close proximity to riparian areas. All of these previous descriptions were primarily qualitative in nature (with the exception of Gonzalez-Medina et al. 2009), did not relate habitat use to habitat availability, and were limited in scope, duration, sample size, and geographic coverage.

Because of the limited information known about winter habitat use by black-capped vireos in Mexico, I initiated a study to determine if habitat characteristics differed between patches known to be used by vireos (i.e., used or occupied patches) and

available, random patches. Specific objectives for this research were to (1) describe habitat characteristics of winter patches used by black-capped vireos, (2) determine what habitat characteristics may influence vireo use of winter patches, and (3) evaluate differences in habitat characteristics between winter patches across different latitudes, elevations, and habitat types at sites across western Mexico, as well as between different age/sex classes.

Methods

Study Location

Field research was conducted over 2 winter periods (31 January 2003–9 April 2003; 8 December 2003–19 March 2004) at study sites located along the Pacific slopes of the Sierra Madre Occidental mountains in western Mexico, and ranging in elevation from sea level to 1500 m (Fig. 2.1, Table 2.1). Sites were located along a north-south gradient in the states of Sinaloa, Durango, Nayarit, Jalisco, Colima, Guerrero, Michoacán, and Oaxaca.

The distribution of the forests of the Sierra Madre Occidental is influenced by climate and physical characteristics of the landscape, including topography, slope, aspect, and soil conditions, which contributes to considerable spatial variation in structure and species composition (Rzedowski 1978, Apan and Peterson 1998, Helmer 2000, Trejo and Dirzo 2000, Galicia et al. 2008). Corresponding to the elevation and topographically-driven differences in water availability, various vegetation types are found along Mexico's Pacific Coast (Maass et al. 2005, Perez et al. 2008). Following

the general descriptions of Miranda and Hernandez (1963), Rzedowski (1978), and Ricker et al. (2007), the 3 broadly defined categories of forest within this region include 1) thorn forest, 2) tropical deciduous and semi-deciduous forest, and 3) pine-oak forest. Thorn forest, tropical deciduous forest, and tropical semi-deciduous forest all fall within the general classification of tropical dry forest. Thorn forest grows in more arid regions at lower altitudes near the coast, whereas deciduous and semi-deciduous forests grow on the relatively more humid hills below the pine-oak woodlands that occur at higher altitudes (Fig. 2.2; Arbingast et al. 1975). Within the ecoregions of Mexico with documented winter occurrence of black-capped vireo, approximately 48% of the original area was comprised of tropical dry forest habitats and 44% was comprised of temperate vegetation formations (e.g., pine and pine-oak forests; Vega Rivera et al. 2010).

Mexico's tropical dry forests are found in dry to subhumid climates (annual average rainfall 600-1200 mm) that are warm (annual average temperature 20-29 degrees C) with highly marked seasonality (5- to 8-month dry season), and that occur at altitudes of 0-1500 m (Miranda and Hernandez 1963, Rzedowski 1978, Trejo 1999, Sanchez-Azofeifa et al. 2005). These forests are typically dominated by deciduous trees (more than 50%) and are predominantly established on moderate to steep slopes with shallow soils (Trejo and Dirzo 2002, Sanchez-Azofeifa et al. 2005).

Thorn forest is the shortest in stature of all dry forests and has an increased presence of thorny plants mainly from the Fabaceae (legume) and Cactaceae (cactus) families (Dirzo 1994). Found at lower altitudes and on gently sloping ground along the Pacific coast, thorn forest consists of tree vegetation of up to 10 m height dominated by

Acacia (acacia) or *Prosopis* (mesquite) genera, with a sparse herb layer (Leopold 1959, Corcuera and Butterfield 1999, Maass et al. 2005, Ricker et al. 2007). Other frequently occurring woody plants include *Parkinsonia* (palo verde), *Olneya* (ironwood), *Pithecellobium*, *Croton*, *Ipomoea* (morning glory), and *Lysiloma* genera. Typical cacti include columnar (Tribe Pachycereeae) and globose (*Mammillaria* spp.) cacti, as well as prickly pears (*Opuntia* spp.; Dirzo 1994).

Tropical deciduous forest and tropical semi-deciduous forest often are considered together because the two vegetation types can be difficult to distinguish from one another (Rzedowski 1978, Cue-Bar et al. 2006). These forests exhibit high diversity and are typical of Mexico's tropical dry forests, with extensive cover of both broad-leaved and small-leaved trees and shrubs (Cue-Bar et al. 2006). They harbor an avian community with more endemic species than any other vegetation type in Mexico and a richness of species approximately equal to that of the tropical rain forests (Escalante et al. 1993). These forests are typically of 4-15 m height, with characteristic genera including *Plumeria* (frangipani), *Bursera*, *Gyrocarpus*, *Guazuma*, *Heliocarpus*, *Ipomoea*, *Lonchocarpus*, *Lysiloma*, *Mimosa*, *Spondias*, and *Pseudosmodingium* (Corcuera and Butterflied 1999, Maass et al. 2005, Cue-Bar et al. 2006, Ricker et al. 2007, Romero-Duque et al. 2007).

Another less prevalent vegetation type is gallery forest, which is conspicuous riparian vegetation that occurs along the margins of intermittent and perennial streams (Lott et al. 1987, Rickers et al. 2007). Gallery forests can establish along riparian areas because the soil humidity is higher than otherwise occurs in the area, allowing woody

species to grow considerably larger (both in height and diameter) than the relatively smaller trees common in tropical dry forests (Dirzo 1994). Typical vegetation includes genera such as *Astianthus*, *Ficus* (fig), *Salix* (willow), and *Taxodium* (cypress; Lott et al. 1987, Rickers et al. 2007).

At the eastern and highest elevation sections (600-2100m) along the Sierra Madre Occidental, mixed oak and pine-oak forests are found, with pine-oak forests consisting of trees up to 20 m height where both *Quercus* (oak) and *Pinus* (pine) genera are present and either one is dominant (Maass et al. 2005, Ricker et al. 2007). Mixed oak forest frequently occurs as an ecotone between the dry forests of the lower altitudes and the pine-oak forests of the higher altitudes, and contains floristic components of both (Dirzo 1994, Maass et al. 2005, Ricker et al. 2007). Mixed oak forest contains trees up to 30 m in height and is dominated by *Quercus* oaks (Corcuera and Zavala-Hurtado 2006, Ricker et al. 2007). The greatest richness of *Quercus* species in the world is found in Mexico, where 90% of the approximately 150 oak species of North America, including 86 endemics, are distributed, especially on the dry Pacific slopes (Nixon 1993, 2006). Half of the world's species of *Pinus* occur in Mexico (Saenz-Romero et al. 2003).

Study sites included all of these vegetation associations along the western slopes of the Sierra Madre Occidental, although survey effort was not distributed equally among them because sampling occurred where black-capped vireos were located. Most sites have been disturbed to some degree by human activities. Tropical dry forest frequently occurs in a mosaic of disturbed secondary vegetation and patches of relatively

undisturbed primary vegetation (Trejo and Dirzo 2000, Gordon et al. 2004, Gove et al. 2005), making it sometimes difficult to distinguish between habitat types (Trejo 1998).

Data Collection

One approach to detect and measure habitat selection is to compare data for specific habitat attributes between areas of documented use and randomly selected areas (e.g., Marcum and Loftsgaarden 1980, Dunn and Braun 1986, Manly et al. 2002). The specific study design I used (the "site attribute design" as described by Garshelis 2000) involves generating a measure of selection by first evaluating several habitat-related attributes at sites used by study organisms and at random sites. Then I identified the variables, and the values of those variables, that best characterize sites that are used by the study organism. In this design, the dependent variable is whether each site was used by the study organism or if it was a random location with unknown use (i.e., a binary response), and the independent variables are the various habitat attributes measured at each site. The site attribute design avoids some of the pitfalls associated with other study designs and also tends to provide stronger inference about habitat selection (Garshelis 2000, Thomas and Taylor 2006). It may also avoid the problem of inferring absence from non-detection in presence-absence studies, which can lead to flawed inference about habitat use because a species may not be detected even if present (e.g., Johnson 1981, North and Reynolds 1996, Mackenzie et al. 2006).

Thus, I compared habitat characteristics between areas of known black-capped vireo use and randomly selected areas representing available habitat where use by black-capped vireos in unknown (unknown occupancy is defined as surveyed locations for

which I did not detect any vireos, similar to the definition of non-detections in a recent study of vireos in Texas by McFarland et al. 2013). Because of the large extent of the region surveyed and the relative scarcity of the endangered focal species, survey sites in many cases were located at sites of potential occurrence based on the literature (e.g., Graber 1961, Marshall et al. 1985, Binford 1989, Hutto 1992, Howell and Webb 1995, Howell 1999) or from amateur and professional birding trip reports.

At study sites, I walked through scrub or forested habitats searching visually for individual black-capped vireos and also seeking auditory clues to their presence, including vocalizations by vireos and members of mixed-species flocks that sometimes associate with black-capped vireos. This approach has been used for winter studies of golden-cheeked warblers, a species in which winter vocalizations by the species are infrequent (e.g., Rappole et al. 1999, 2000). Wintering black-capped vireos tend to be among the least audible and detectable species, and are not active flock participants, but sometimes appear in the vicinity of winter flocks. Typical flock members include Wilson's warbler, blue-gray gnatcatcher, MacGillivray's warbler, Nashville warbler, orange-crowned warbler, plumbeous vireo, warbling vireo, and varied bunting. Gonzalez-Medina et al. (2009) most often found black-capped vireos in Sinaloa to be solitary, but when other species were present, they included orange-crowned warblers, Wilson's warblers, and warbling vireos.

At each point of known black-capped vireo occurrence, I established a 0.04-hectare (ha) circular plot (i.e., 11.3 m radius), centered on the tree or shrub in which the focal bird was initially observed, to determine habitat composition (James and Shugart

1970, Stoddard and Stoddard 1987). Additionally, the same measurements were taken at 3 additional subpoints, each centered 35 m from the first subpoint (the original location of each focal vireo) and 120 degrees from one another (Fig. 3.1). For comparison, I collected the same measurements at 3 randomly selected locations along the survey transect at each surveyed site containing black-capped vireos.

To characterize the habitat characteristics of areas known to be used by black-capped vireos, I combined data from the 4 subpoints centered on each patch of known black-capped vireo use (i.e., the vireo point + the 3 subpoints centered on it) to calculate a single mean value with confidence intervals for each variable. To characterize the habitat characteristics at random plots with unknown use by black-capped vireos, I similarly combined the data from the 3 random plots to produce a single mean value with confidence intervals for each variable. Thus, I could evaluate habitat composition by directly comparing a single composite value for use sites to one for random sites for each habitat variable.

By extending the evaluation of black-capped vireo "use" patches to the 4 subpoints, as opposed to the single point of initial occurrence, my intent was to capture more of the variability in the habitat around the area of known use. The home range or territory is an appropriate scale of study for habitat selection by a territorial animal (e.g., Johnson 1980, Manly et al. 2002). My approach allows for analysis of vegetation composition from 4 locations within a 0.67 ha area (i.e., radius of the composite circular

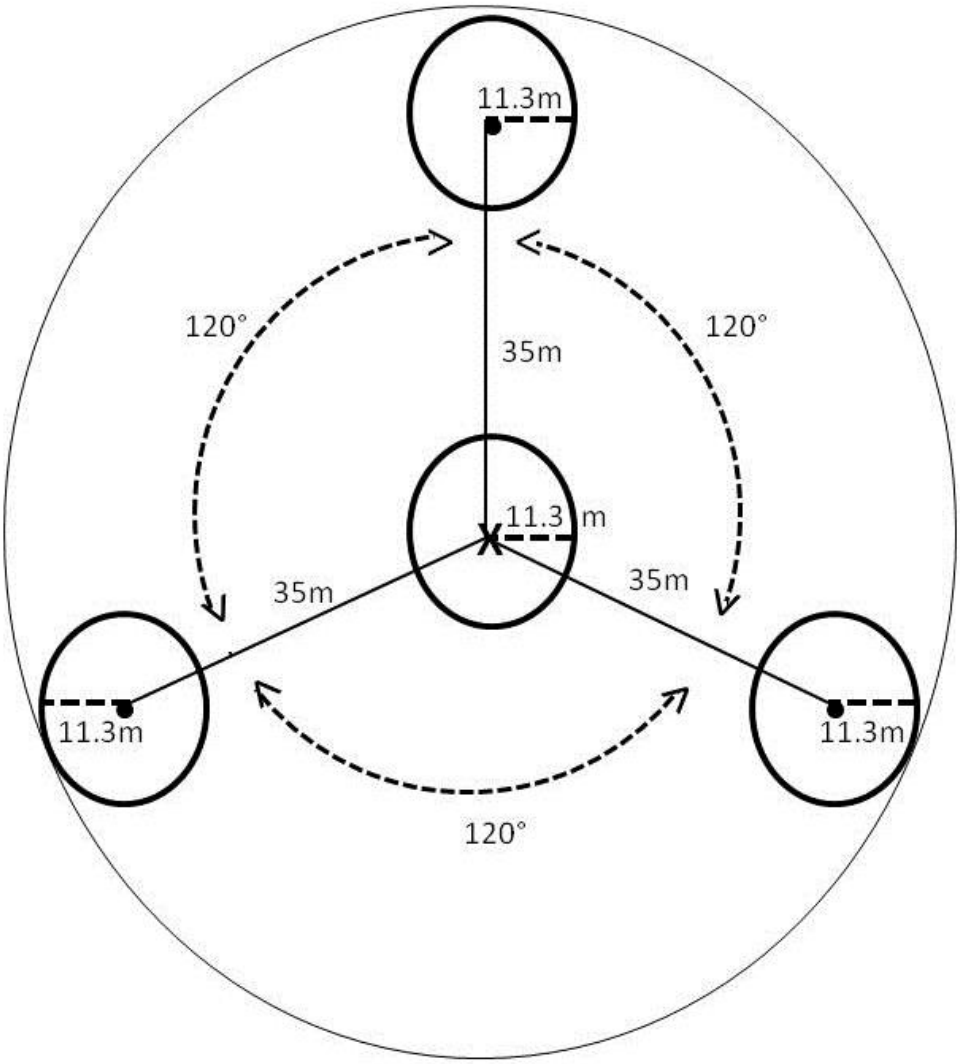

Figure 3.1. Spatial arrangement for vegetation subplots at each black-capped vireo location. The X at the center of the middle plot marks the location of first observation of a vireo. Habitat characteristics are measured within each of the 4 0.04-ha subpoints. The 3 subpoints around the perimeter are each located 35m from the center point and 120 degrees from one another, where the first of the 3 is selected in a random location from the center point. Habitat characteristics for the vireo plot are combined to form a single composite value for each variable.

plot = 35 m + 11.3 m = 57.6 m), which I assumed is a reasonable approximation of the area likely used (i.e., the home range) by vireos, considering the best scale for predicting vireo breeding suitability (0.05-0.25 ha; Wilsey et al. 2012) and their territory size during the breeding season (i.e., 1.0-2.0 ha; Graber 1961). The vegetation sampling procedure used within each 0.04-ha plot is a modified version of the James and Shugart (1970) method for sampling vegetation in forest and shrub systems (Stoddard and Stoddard 1987, Martin et al. 1997). Variables measured within each plot include two measures of topography (aspect (i.e., compass direction) and slope), two measures of tree structure (canopy cover, mean tree diameter at breast height [DBH]), and three measures of shrub structure (mean shrub distance, mean tree distance, and foliage density). I measured percentage of canopy cover (i.e., forest overstory density) with a spherical densitometer. Mean shrub distance and mean tree distance are measures of shrub and tree density, respectively (i.e., plant density [plants/ha] = 1/[mean plant distance^2] x 10,000).

I used a Nudds density board to assess horizontal foliage density (i.e., understory cover) at the 4 cardinal directions 11.3m from the center of each plot (Nudds 1977). Foliage density, a measure of foliage structure, describes in this study the percent of a 2.5m graduated density board that is obscured by foliage when viewed from an 11.3m distance. I used ocular estimates to determine the percent of foliage obscured, placing estimates into one of 6 classes (1 = 0–5% cover, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, 6 = 96–100%), for each of 8 panels on the board, yielding a maximum possible score of 192 for any individual plot (i.e., 8 panels x 4 directions x maximum

value of 6 = 192). I qualitatively considered values <25% to indicate minimal understory vegetative cover, compared to sparse (26–50%), moderate (51–75%), and dense (76–100%) cover.

I also looked for differences in the habitat characteristics of patches used by black-capped vireos at different latitudes and altitudes, and between different age/sex categories. Groups included 3 classes of latitude (sites < 21, 21–23, > 23 degrees latitude), 3 classes of elevation (< 400 m, 400–1000 m, > 1000 m), 2 classes of sex/age (adult male, all others), and 2 classes of habitat type (thorn forest and tropical deciduous and tropical semi-deciduous forest). Latitudes > 23 degrees (i.e., 23–25) correspond to the northernmost sites (all sites in Sinaloa and Durango states), sites 21–23 degrees latitude correspond to most of the state of Nayarit (all sites north of Sayulita), and sites < 21 degrees (i.e., 19–21) correspond to all sites south of, and including, Sayulita, Nayarit, and includes all sites in Jalisco and Colima states. Although some black-capped vireos were located in riparian gallery forest or mixed oak woodlands, there were not enough records of these occurrences for inclusion in statistical evaluations, and so I did not include those records in the statistical analysis of habitat types. Because wintering black-capped vireos cannot be easily classified by age and sex in the field (see Chapter II), I compared habitat characteristics between known adult males and all other vireos (which includes females and all juveniles). Despite the limitations of this, it is the most conservative approach, it increases the sample size, and it still reveals meaningful patterns because differences in habitat use generally result from patterns of male

dominance over "subordinate" individuals, including both females and younger birds (e.g., Gauthreaux 1982, Lundberg 1985, Lynch et al. 1985, Wunderle 1992).

Data Analysis

To determine which patch characteristics had the greatest influence on the probability of black-capped vireo winter habitat use, I used generalized linear regressions and model likelihood estimates to relate explanatory habitat variables to black-capped vireo site use. For the analysis, I classified habitat sites as 1 if the site was known to be used by black-capped vireos, and 0 if otherwise. I used an information theoretic approach to evaluate the relative fit of a suite of potential models (dependant variable = black-capped vireo site use; independent variables = candidate models) following Burnham and Anderson (2002).

I used SPSS software (Release 15.0.0, 2006) to run a small number of *a priori* model sets fitted to a binomial distribution (Burnham and Anderson 2002). To evaluate the effect of habitat characteristics on the probability of black-capped vireo site use, I evaluated a set of *a priori* models, including a global model containing all 7 parameters, 8 reduced models (subsets of the global model) considered plausible alternatives, and an intercept-only (null) model using Akaike's Information Criterion corrected for small sample size (AIC_c, Burnham and Anderson 2002). I ranked and compared models using ΔAIC_c, which is an estimate of the distance between the best-approximating model and model *i* for the set of models considered (Buckland et al. 1997, Burnham and Anderson 1998). I considered all models within 2 AIC_c units of the best model as competing models for explaining black-capped vireo site use, and models with $\Delta AIC_c > 2$ were

poor representations of the data (Burnham and Anderson 1998, Burnham and Anderson 2002).

Because the selection of *a priori* candidate models is based on what is known or hypothesized about a system under study, and is at least a partially subjective process, there is a likelihood that some good models were not initially considered, justifying the construction of additional *a posteriori* models (Burnham and Anderson 2002, Norman et al. 2004, McCleery et al. 2007). After eliminating the *a priori* models with $\Delta AIC_c > 2$ from further consideration, I evaluated the individual parameters for all remaining *a priori* models and selected all parameters that were significant ($P \leq 0.05$) in at least one model for construction of 14 *a posteriori* models. I again used the relative difference to the smallest AIC_c in each model set to select the best approximating models, and compared the results of the *a priori* and *a posteriori* tests to select the best model using ΔAIC_c and Akaike weights (w_i) (Burnham and Anderson 2002).

To evaluate the influence of the individual variables in the best model on the probability of black-capped vireo patch use, I fit a logistic regression equation function for the probability of use as a function of the habitat variables in the best fitting model (i.e., a resource selection probability function; Manly et al. 2002). Specifically, I exponentiated the binomial regression analysis of the selected model and derived a prediction equation (Agresti 2007, Guthery and Bingham 2007). To plot the effect of each covariate on black-capped vireo habitat patch use, I held the other covariates in the exponentiated equation constant at their average and allowed the plotted covariate to vary throughout its range (Schmidt et al. 2010).

I used 1-way analysis of variance (ANOVA) to compare means of variables among habitat patches used by black-capped vireos grouped by latitude, elevation, sex/age, and habitat type. When ANOVA results indicated a significant ($P \leq 0.05$) difference between groups (if > 2 groups were included), I identified which pairs were different using the *post hoc* least significant difference test (i.e., Fisher's LSD test) with an alpha value set at 0.05.

Results

I evaluated habitat characteristics in 56 patches containing black-capped vireos over the course of the study, including 13 locations in 2002–2003[2] and 43 in 2003–2004. Additionally, habitat characteristics were evaluated at 168 subpoints (i.e., 3 associated with each BCVI subpoint), and at 93 random points (i.e., 31 unique study sites with known black-capped vireo occurrence x 3 random plots evaluated per site = 93).

Relative to the random patches, I found habitat patches with known black-capped vireo use to occur on steeper, more south-facing slopes, with vegetation of lower percent canopy cover, greater foliage density, and higher densities of shrubs (Table 3.1). Non-overlapping confidence intervals for both slope and foliage density indicate statistically significant ($P \leq 0.01$) differences between the means, and the variables aspect, canopy cover, and shrub distance also demonstrated statistically significant differences ($P \leq 0.05$; Table 3.1).

[2] No fieldwork was conducted in 2002 during the 2002-2003 winter (fieldwork began in January 2013), but I still refer to that winter as 2002-2003 as a conventional description of the entire winter period.

Table 3.1. Mean and 95% confidence intervals (CI) for patch characteristics hypothesized to influence winter habitat use of black-capped vireos in western Mexico, 2003–2004.

	BCVI Use (*n*=56)		Available Sites (*n*=31)	
Predictor [a]	$\bar{x}$	(*95% CI*)	$\bar{x}$	(*95% CI*)
Slope	21.8	18.5–25.1	10.2	6.7–13.7
Asp	172.4	152.2–192.6	135.7	118.7–152.7
CnCv	70.4	65.9–74.9	82.6	74.6–90.6
FD	141.5	133.6–149.3	101.6	91.2–111.9
TrDBH	25.9	22.8–29.0	31.4	26.9–35.9
ShDis	2.4	2.0–2.8	3.8	2.8–4.8
TrDis	12.9	11.3–14.5	14.9	11.6–18.2

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m).

Among the *a priori* models, I found model 1 (the global model) best approximated the data, and models 2-4 were competing models (i.e., all had $\Delta AIC_c < 2$; Table 3.2). From those 4 candidate models, I generated 14 *a posteriori* models (all combinations of the 4 variables with significant parameters among the competing *a priori* models). Among the *a posteriori* models, I found model 11 best approximated the data, and there were no other *a posteriori* models considered as competing alternatives (Table 3.2). The w_i for model 11 was 0.60, indicating there is an 60% probability model 11 is the actual best model of the set and provides the best explanation of the data (Burnham and Anderson 2002). This is strong weight of evidence for model 11, which is 2.9 times more likely to be the best explanation for black-capped vireo winter patch use than the next best *a posteriori* candidate model (i.e., model 12; 0.60/0.21=2.9).

Comparing the best *a priori* models (models 1–4; Table 3.2) to model 11, only models 1 and 2 had lower AIC_c values, although the AIC_c values were very close ($\Delta AIC_c < 1$) for all 3 of these models. Because model 1 has 3 additional parameters in the model (i.e., 8 parameters vs. 5 in model 11), its slightly lower AIC_c value is a product of the larger number of parameters and should not be considered a better overall model than model 11 (Burnham and Anderson 2002). Model 2 also should not be considered a better overall model because the 95% *CI* for one of the parameters in the model (aspect) contained 0 ($\hat{\beta}$ = 0.010; 95% *CI* = -0.002 to 0.210), indicating it was not a relevant predictor of black-capped vireo winter habitat patch use. Thus, I consider model 11 the best overall model.

Examining the individual parameter estimates and 95% *CI*'s for parameters in

Table 3.2. *A priori* and *a posteriori* models correlating black-capped vireo winter habitat patch use to patch characteristics at sites in western Mexico, 2003–2004. This table contains number of parameters (K), -2*natural log of the maximum likelihood estimate (-2ln*L*), Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), and Akaike weights (w_i) for each model.

Model [a]		K	-2ln*L*	AIC_c	ΔAIC_c	w_i
a priori						
1	Global	8	59.86	78.48	0.0	0.30
2	Slope+Asp+TrDBH+CnCv	5	67.55	78.59	0.1	0.29
3	Slope+Asp+FD+TrDBH	5	68.21	79.41	0.9	0.19
4	Slope+Asp+FD+CnCv	5	69.22	80.25	1.8	0.13
5	Slope+FD+CnCv	4	72.85	81.49	3.0	0.07
6	Slope+Asp+FD+ShDis	5	72.43	83.63	5.1	0.02
7	FD+ShDis+TrDis+TrDBH	5	78.72	89.85	11.4	0.00
8	Slope+Asp+ShDis+TrDis	5	79.17	90.37	11.9	0.00
9	Null	1	94.03	96.10	17.6	0.00
10	Slope+ShDis+TrDis	4	89.33	98.07	19.6	0.00
a posteriori						
11	Slope+CnCv+FD+TrDBH	5	68.40	79.37	0.0	0.60
12	Slope+FD+CnCv	4	72.85	81.49	2.1	0.21
13	CnCv+FD+TrDBH	4	73.89	82.53	3.2	0.12
14	CnCv+FD	3	79.79	86.16	6.8	0.02
15	FD+TrDBH	3	80.34	86.78	7.4	0.01

Table 3.2 continued

Model [a]		K	-2ln*L*	AIC_c	ΔAIC_c	w_i
a posteriori						
16	Slope+FD	3	80.37	86.81	7.4	0.01
17	Slope+CnCv+TrDBH	4	80.23	88.86	9.5	0.01
18	Slope+CnCv	3	83.23	89.60	10.2	0.00
19	FD	2	85.81	90.05	10.7	0.00
20	Slope+TrDBH	3	89.49	95.93	16.6	0.00
21	Slope	2	92.35	96.59	17.2	0.00
22	CnCv+TrDBH	3	97.31	103.69	24.3	0.00
23	CnCv	2	102.76	106.95	27.6	0.00
24	TrDBH	2	105.74	109.95	30.6	0.00

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m); global = model containing all 7 variables; null = intercept only.

model 11, none of the parameters contained 0, suggesting all were relevant predictors of vireo winter patch use (Table 3.3). For model 11, I found a positive correlation between black-capped vireo winter patch use and both slope (Table 3.3, Fig. 3.2a) and foliage density (Table 3.3, Fig. 3.2b), and a negative correlation between black-capped vireo winter patch use and both canopy cover (Table 3.3, Fig. 3.2c) and tree DBH (Table 3.3, Fig. 3.2d). Patches used by black-capped vireos were, on average, on terrain of 22 degree slope with 70% canopy cover, moderate to dense understory cover (i.e., foliage density = 142), and 26 cm tree DBH, compared to random available patches that were on terrain of 10 degrees slope with 83% canopy cover, sparse to moderate understory cover (i.e., foliage density = 102), and 31 cm tree DBH (Table 3.1).

Results of the ANOVA tests for latitude indicate that 2 of the 7 variables (canopy cover, shrub distance) differed significantly between latitude groups ($P \leq 0.05$; Table 3.4). *Post hoc* comparisons indicate that canopy cover was higher at sites above 23 degrees latitude than at sites 21–23 degrees latitude, and canopy cover was higher and shrub distance was lower (i.e., shrub density was greater) at sites below 21 degrees latitude than at sites 21–23 degrees latitude (Table 3.5). There were no significant differences between the elevation groups for any variable based on ANOVA comparisons (Table 3.6). Results of the analysis of sex/age groups revealed a significant difference only for aspect, which was higher for adult males (189.7, south-facing slopes) than for all other birds (149.0, southeast-facing slopes; Table 3.7). Comparisons between habitat types indicated statistically significant differences for 3 of the 7 variables ($P \leq 0.05$; Table 3.8). Vireo habitat plots classified as thorn forest had greater

Table 3.3. Model parameter estimates ($\hat{\beta}$) and 95% confidence intervals relating black-capped vireo winter habitat patch use to patch characteristics at sites in western Mexico, 2003–2004. Positive $\hat{\beta}$ values indicate a positive relationship, and negative $\hat{\beta}$ values indicate a negative relationship between the parameter and black-capped vireo winter habitat patch use.

Parameter [a]	$\hat{\beta}$	95% *CI*
Slope	0.071	0.008 to 0.134
CnCv	-0.041	-0.071 to -0.010
FD	0.033	0.011 to 0.054
TrDBH	-0.049	-0.097 to -0.002

[a] Variable notation for patch attributes: Slope = slope (degrees); CnCv = canopy cover (percent); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); and TrDBH = mean tree diameter-at-breast-height (cm).

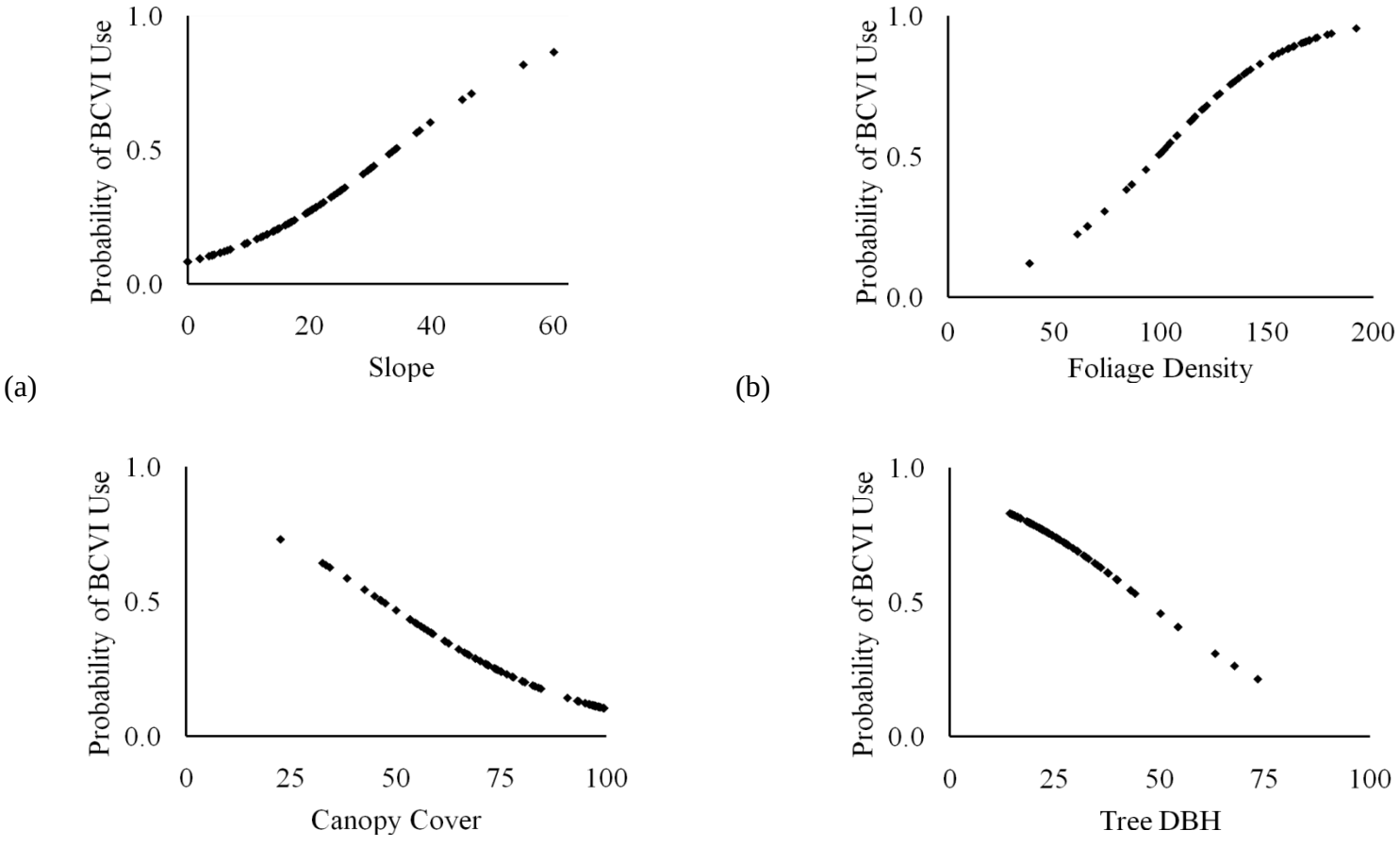

Figure 3.2. Probability of black-capped vireo winter habitat patch use predicted as a function of (a) slope (degrees); (b) foliage density (0-192, 0 = 0%, 192 =100% cover); (c) canopy cover (percent); and (d) tree diameter-at-breast-height (cm) for sites in western Mexico, 2003–2004.

Table 3.4. Means, standard errors (SE), *F*-ratios (*F*), and *P*-values (*P*) for each variable among different latitude groups of habitat patches used by black-capped vireos at sites in western Mexico, 2003–2004. Asterisks (*) indicate statistically significant differences ($P \leq 0.05$) between groups.

Variable [a]	Lat > 23 deg	Lat 21–23 deg	Lat < 21 deg	ANOVA
	Mean (SE)	Mean (SE)	Mean (SE)	*F* (*P*)
Slope	26.5 (3.3)	19.8 (2.0)	17.8 (3.2)	2.52 (0.091)
Asp	172.9 (20.3)	182.3 (15.3)	154.7 (17.4)	0.54 (0.587)
CnCv	75.3 (2.9)	63.7 (3.6)	75.1 (5.3)	3.24 (0.048)*
FD	140.6 (8.4)	133.6 (5.7)	155.9 (5.2)	2.60 (0.084)
TrDBH	21.8 (1.7)	26.4 (2.6)	30.4 (3.8)	2.15 (0.127)
ShDis	2.5 (0.4)	2.8 (0.4)	2.4 (0.2)	3.23 (0.048)*
TrDis	15.0 (1.5)	11.2 (0.9)	13.1 (1.8)	2.22 (0.120)

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m).

Table 3.5. Results of *post hoc* least significant difference test (i.e., Fisher's LSD test) for variables found to have significant ($P \leq 0.05$) differences between groups in Table 3.4. $\bar{x}_1$ represents means of variables for black-capped vireo use patches with latitude > 23, $\bar{x}_2$ represents that for patches 21–23 degrees latitude, and $\bar{x}_3$ represents that for patches < 21 degrees latitude. Mean differences are presented between individual groups, along with standard errors (SE) and *P*-values (*P*) set at an alpha level of 0.05. Asterisks (*) indicate statistically significant differences ($P \leq 0.05$) between groups.

Variable [a]	$\bar{x}_1 - \bar{x}_2$ (SE)	*P*	$\bar{x}_1 - \bar{x}_3$ (SE)	*P*	$\bar{x}_2 - \bar{x}_3$ (SE)	*P*
CnCv	11.58 (5.1)	0.029*	0.20 (5.9)	0.973	-11.38 (5.7)	0.050*
ShDist	-0.34 (0.5)	0.472	0.95 (0.5)	0.080	1.28 (0.5)	0.015*

[a] Variable notation for patch attributes: CnCv = canopy cover (%); ShDis = Mean distance to nearest shrub within plot (m).

Table 3.6. Means, standard errors (SE), *F*-ratios (*F*), and *P*-values (*P*) for each variable among different elevation groups of habitat patches used by black-capped vireos at sites in western Mexico, 2003–2004.

Variable [a]	< 400 m	400- 1000 m	> 1000 m	ANOVA
	Mean (SE)	Mean (SE)	Mean (SE)	*F* (*P*)
Slope	19.5 (2.4)	26.0 (2.9)	18.4 (3.6)	2.02 (0.143)
Asp	162.3 (15.9)	194.5 (16.5)	148.9 (21.5)	1.62 (0.207)
CnCv	69.3 (4.1)	70.8 (3.1)	72.4 (5.1)	0.12 (0.888)
FD	148.2 (6.0)	131.4 (6.7)	143.3 (8.3)	1.81 (0.174)
TrDBH	24.4 (2.6)	24.0 (1.6)	32.6 (4.5)	2.20 (0.121)
ShDis	2.6 (0.4)	2.4 (0.2)	1.8 (0.4)	0.88 (0.423)
TrDis	13.9 (1.3)	12.0 (1.3)	12.4 (1.3)	0.61 (0.546)

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m).

Table 3.7. Means, standard errors (SE), *F*-ratios (*F*), and *P*-values (*P*) for each variable among different sex/age groups of habitat patches used by black-capped vireos at sites in western Mexico, 2003–2004. Asterisks (*) indicate statistically significant differences ($P \leq 0.05$) between groups.

Variable [a]	Adult Males [b]	All Others [c]	ANOVA
	Mean (SE)	Mean (SE)	*F* (*P*)
Slope	22.2 (2.4)	21.3 (2.4)	0.07 (0.796)
Asp	189.7 (15.1)	149.0 (11.7)	4.05 (0.049)*
CnCv	69.8 (3.1)	71.3 (3.5)	0.10 (0.749)
FD	138.3 (5.3)	145.4 (6.2)	0.77 (0.383)
TrDBH	25.4 (1.8)	26.5 (2.9)	0.11 (0.742)
ShDis	2.4 (0.3)	2.4 (0.4)	0.02 (0.893)
TrDis	12.3 (1.1)	13.8 (1.1)	0.88 (0.353)

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m).
[b] Adult males refers to all birds identified as adult males in the field and may not necessarily include all adult males because sexing birds is not reliable for second year or after hatch year adults (Pyle 1997).
[c] All others refers to all birds not identified as adult males and thus potentially includes all females, juveniles, and some adult males unidentified as such.

Table 3.8. Means, standard errors (SE), *F*-ratios (*F*), and *P*-values (*P*) for each variable among different habitat type groups for patches used by black-capped vireos at sites in western Mexico, 2003–2004. Asterisks (*) indicate statistically significant differences between groups at the $P \leq 0.05$ threshold, and double asterisks (**) indicate statistically significant differences between groups at the $P \leq 0.10$ threshold.

Variable [a]	Thorn Forest	Deciduous Forest [b]	ANOVA
	Mean (SE)	Mean (SE)	*F* (*P*)
Slope	17.3 (2.4)	23.1 (2.2)	2.51 (0.120)
Asp	161.8 (16.3)	176.6 (12.3)	0.47 (0.498)
CnCv	48.2 (8.6)	65.6 (4.5)	3.89 (0.055)**
FD	154.2 (6.4)	135.7 (4.9)	4.97 (0.031)*
TrDBH	20.4 (1.5)	29.2 (2.3)	6.47 (0.014)*
ShDis	1.6 (0.2)	2.7 (0.3)	6.93 (0.011)*
TrDis	14.2 (1.8)	12.1 (0.9)	1.36 (0.249)

[a] Variable notation for patch attributes: Slope = slope (degrees); Asp = slope aspect (degrees); TreeDBH = mean tree diameter-at-breast-height; CnCv = canopy cover (%); FD = vertical foliage density (0-192, 0 = 0%, 192 =100% cover); ShDis = Mean distance to nearest shrub within plot (m); TrDis = Mean distance to nearest tree within plot (m).

[b] Deciduous forest represents all locations classified as either tropical deciduous forest or tropical semi-deciduous forest.

foliage density, higher shrub density, and smaller tree DBH than habitat classified as tropical deciduous forest or tropical semi-deciduous forest. Additionally, thorn forest had less canopy cover than tropical deciduous or semi-deciduous forests ($P = 0.055$; Table 3.8), which is statistically significant at the $P \leq 0.10$ threshold.

Discussion

Black-capped vireo winter habitat use was best predicted by increasing values of slope and foliage cover, and by decreasing values of canopy cover and tree DBH in this study (model 11, Table 3.2; Fig. 3.2). The difference between patches of known vireo use and random sites was most pronounced for slope; vireos were found in patches with slopes more than twice as steep as those of random sites (mean = 21.8 vs. 10.2, respectively; Table 3.1). Although there is a negative correlation between black-capped vireo winter patch use and canopy cover (Table 3.3, Fig. 3.2b), vireos nevertheless selected patches with moderately high canopy cover (i.e., mean canopy cover = 70.4% for vireo sites, compared to 82.6% for random sites; Table 3.1). In general, vireos used winter sites that occur on steeper, more south-facing slopes, with vegetation of lower percent canopy cover, greater foliage density, and higher densities of shrubs than what is available.

The importance of slope for black-capped vireos is consistent with patterns observed for the species in some parts of the breeding range, as well as what is known about their wintering habitat. During the breeding season, the black-capped vireo is often found occupying steep slopes, such as the heads of ravines or along the sides of

arroyos (Ratzlaff 1987). Recent range-wide investigations of habitat use by black-capped vireos demonstrated that detection locations occurred on steeper slopes than non-detection locations across much of the breeding range (McFarland et al. 2012). Graber (1961) proposed that the rugged terrain fosters microclimates that perpetuate clumping of vegetation and the shallow soils on these steeper slopes slowed plant succession, which allows vegetation to remain in a suitable stage for vireos. However, this explanation might not be appropriate regarding wintering occupancy because the habitat requirements of the species during the winter are more relaxed than during the breeding season (e.g., Graber 1961, Gonzalez-Medina et al. 2009, this study), which may include less need for trees of a certain successional stage.

An alternative explanation for vireo use of steeper slopes is that vegetation on the steep slopes persists more than it does on less rugged terrain because conversion to agriculture is more likely on the latter (Vega Rivera et al. 2010). Trejo and Dirzo (2000), for example, found that landscapes with slopes less than 12 degrees are most heavily used for agricultural purposes, whereas landscapes on steeper slopes (especially when greater than 45 degrees) undergo the lowest deforestation rates and thus serve as a refuge for tropical dry forest in Mexico. Similarly, Galicia et al. (2008) found that the most inaccessible areas and steepest slopes were the least used areas for agriculture, and stated that most remaining primary tropical dry forest of Mexico is located in valleys and ravines. Thus, black-capped vireos, and other species, may be restricted to steeper slopes simply because few other options exist in the heavily modified landscapes of western Mexico.

In addition to use of steeper slopes, black-capped vireos also used more south-facing slopes than what was available. This also is consistent with some patterns observed on the breeding grounds. For example, black-capped vireos are frequently found breeding in habitat on south-facing slopes at the Balcones Canyonlands Preserve in Austin, Texas (LCRA 2007), and vireos were found at higher densities on south-facing slopes in northern Coahuila, Mexico than on other slopes (Benson and Benson 1990, 1991).

One possible explanation for a preference for south-facing slopes has to do with the influence of patterns of incoming solar radiation on vegetation. Topography has a major influence on the distribution of incoming solar radiation and hydrologic processes across a landscape (Nichols et al. 1998, Yeakley et al. 2000, Pierce et al. 2005, Suzaki et al. 2005, Gallardo-Cruz et al. 2009). Patterns of incoming solar radiation cause shifts in available energy and water balance conditions, which in turn influence patterns of vegetation structure and diversity (e.g., Armesto and Martinez 1978, Franklin et al. 2000, Martinez-Yrizar et al. 2000, Urban et al. 2000, Vogiatzakis et al. 2003). In the northern hemisphere, slopes facing the Equator (i.e., south-facing slopes) receive more solar radiation than north-facing slopes; therefore, the former tend to be warmer, and consequently drier, than the latter because the greater influx of solar energy results in more water evaporation (Pianka 2000, Gallardo-Cruz et al. 2009). Vegetation thus tends to be better developed on north-facing slopes, especially in relatively dry regions of the Northern Hemisphere, such as the seasonally dry regions of tropical latitudes (Huggett 1998, Beaty and Taylor 2001, Sternberg and Shoshany 2001). In western Mexico, these

patterns produce differences in floristic composition between slopes, such as better developed vegetation on the north-facing slopes relative to those facing south (Gallardo-Cruz et al. 2009).

In this study, vireos used winter sites with vegetation of lower percent canopy cover than what was available, so the relatively less developed vegetation on south-facing slopes may favor vireo occupancy by limiting canopy cover to a suitable level. Interestingly, this pattern of vireo occupancy of relatively open habitats on the wintering grounds is not unlike patterns observed for vireo territories across much of the breeding range (e.g., Graber 1961, Grzybowski et al. 1994, Grzybowski 1995).

Black-capped vireo use of sites with vegetation of lower percent canopy cover, greater foliage density, and greater shrub density may relate to the availability of food resources (i.e., arthropods) during the dry season in western Mexico. Despite generally low arthropod abundance during the winter months (e.g., Janzen and Schoener 1968, Janzen 1973, Hespenheide 1980, Greenberg 1995, Strong and Sherry 2000), there may be differences between vegetation strata that may influence avian use of these strata for foraging. For example, working in an Australian savanna woodland ecosystem, Bell (1985) found that arthropod abundance was less negatively affected by drought conditions in the shrub layer than in the tree layer, and reasoned that the dense and shaded nature of the shrub layer (the foliage of *Acacia* shrubs, in particular), provided a more favorable microclimate for arthropods during periods of water stress than that provided by many taller canopy trees. In Nicaragua, Greenberg and Bichier (2005)

similarly indicated that the greater preponderance of small arthropods in acacia relative to oaks was probably related to the small leaflet size of acacias.

If a similar dynamic occurs in the tropical dry forests of western Mexico, whereby the microclimate of shrubs is more favorable than that of canopy trees for arthropods during dry conditions, then these relative differences in arthropod abundance may influence foraging patterns by insectivorous, foliage-gleaning birds, such as the black-capped vireo. More open forest canopies (i.e., lower canopy cover) allow more light to penetrate to the understory of seasonally dry forests, resulting in greater shrub abundance (Vasquez and Givnish 1998). Thus, sites with lower canopy cover, greater foliage density, and greater shrub density may foster greater abundance of arthropods that black-capped vireos favor. In this study, black-capped vireos foraged at low to medium levels of the foliage ($\bar{x}$ = 2.37 m*; 95% CI* = 2.01 to 2.73), a height range more indicative of foraging in shrubby vegetation than in tree vegetation of taller heights. These foraging heights are similar to what has been observed for black-capped vireos on the breeding range (e.g., $\bar{x}$ = 1.65 m for females, $\bar{x}$ = 3.23 m for males; Houston 2008).

Distinct foliage structures and arthropod populations associated with different vegetation components leads to marked foraging preferences of insectivorous birds (Greenberg and Bichier 2005). Many studies have demonstrated the association between insectivorous birds, foliage structure, and arthropod populations in temperate forests (e.g., Balda 1969, Morse 1976, Holmes and Robinson 1981, Peek 1989, Parrish 1995), although few studies have examined similar patterns in tropical habitats (Greenberg and Bichier 2005). Selection of vegetation for foraging by avian insectivores is primarily a

function of the interaction between abundance of preferred prey, foraging technique, and foliage structure (Holmes and Robinson 1981, Holmes and Schultz 1988). Several studies have demonstrated far higher abundance of small, migratory, insectivorous birds at lower and drier sites than at higher, more mesic sites (e.g., Hutto 1989, Greenberg et al. 1997, Greenberg and Bichier 2005). Greenberg and Bichier (2005) attributed this to the far greater abundance and biomass of small arthropods in the lower, thornier habitats that are favored by small birds (e.g., Thiollay 1988). Additionally, because migratory species do not require large arthropods for reproduction during the nonbreeding period, they can exploit resources that resident birds cannot because resident bird populations typically are restricted by the abundance of large soft-bodied arthropods during the breeding season (Greenberg 1995). Thus, resident birds generally occupy the more mesic sites where there is a higher ratio of large arthropod biomass to total arthropod biomass during the breeding season, allowing the migratory species to exploit the surplus of smaller arthropods at the thornier, more arid sites (Greenberg and Bichier 2005).

Foliage quality plays a role in the higher abundance of arthropods in thorny plants such as acacia because their foliage contains higher levels of nutrients important to arthropods and lower levels of chemical defenses (i.e., condensed tannins) than does oak foliage (Greenberg and Bichier 2005). Acacia and other thorny plants grow in conditions of high grazer and browser intensities and thus invest in mechanical defenses (i.e., thorns), which are an effective defense against vertebrate herbivores, but provide poor protection against arthropod herbivores (Cooper and Owen-Smith 1986, Greenberg

et al. 1997). Thus, thorny plant communities generally have higher arthropod abundance and biomass than oak woodlands because the high tannin content of oaks makes them less palatable to arthropods. If food supply is an important limiting factor for Neotropical migratory birds during the nonbreeding season (e.g., Willis 1966, Cox 1985, Ricklefs 1992, Greenberg 1995, Sherry et al. 2005), then the greater capacity for food acquisition provided by the thorny plants of tropical dry forests provides a viable explanation for why small migrants, such as the black-capped vireo, use these forests relatively more often than other vegetation types.

Arthropod abundance is known to decline in tropical deciduous forests as the dry season advances (Janzen 1973, Wolda and Wright 1992, Lefebvre et al. 1994, Parrish and Sherry 1994), which is why food may be a particularly limiting factor for migratory birds during the late-winter dry season (Sherry et al. 2005, Brown and Sherry 2006b, Johnson et al. 2006, Rockwell et al. 2012). The late-winter dry season is a critical time for migrants because of the need for pre-migratory "fattening" in order to survive migration, arrive at breeding areas in optimal condition, and arrive as early as possible (Brown and Sherry 2006b, Marra et al. 1998, Norris et al. 2004). The decline in arthropod abundance results from the concurrent decline in rainfall as the dry season progresses, which influences food availability for birds and may negatively affect physical condition prior to migration and delay spring departure schedules (Studds and Marra 2007, Rockwell et al. 2012). Delays in arrival can reduce reproductive success by preventing access to high-quality breeding habitat (Gunnarsson et al. 2006) or by limiting time available for replacement of failed clutches (Norris et al. 2004).

Because timing of rainfall during the dry season is important (i.e., rainfall late in dry season increases arthropod availability prior to avian migration), and because amount and timing of rainfall can vary spatially or between habitat types, species in which there are sex or age-related differences in winter habitat use may exhibit differential responses to rainfall patterns among different sex and age classes (Studds and Marra 2007, Rockwell et al. 2012). Thus, research on the relationships between rainfall, food availability, body condition, spring departure and arrival dates, survival and reproductive success is needed for the black-capped vireo, especially considering the segregation between sex and age classes on the wintering grounds described in this study (Chapter II).

I found differences in winter habitat characteristics between black-capped vireos grouped by latitude, sex/age, and habitat type, but none for elevation groups (Tables 3.4–3.8). In comparisons of sex/age groups, adult males were found on more south-facing slopes than all other birds (Table 3.7). As I discussed above, the relatively less developed vegetation on south-facing slopes may favor vireo occupancy; therefore, the greater use of such slopes by adult male vireos may indicate dominance by adult males in selection of more suitable habitat.

Canopy cover was lower at sites 21–23 degrees latitude (including all of Nayarit above the town of Sayulita) than in all other sites (Table 3.5). Vireo plots classified as thorn forest habitat had greater foliage density, greater shrub density, less canopy cover, and smaller tree DBH than plots classified as tropical deciduous forest or tropical semi-deciduous forest (Table 3.8). These results make intuitive sense; thorn forest is

considered a more open (i.e., fewer trees, less tree cover) and shrubby habitat than other vegetation types. Thus, one would expect less canopy cover and greater indicators of shrub presence (e.g., high foliage density, high shrub density) in thorn forest, as well as smaller tree size (i.e., tree DBH) because the drier, warmer environment near the coast results in more stunted growth compared to more mesic sites.

In comparisons between plots at different latitudes, canopy cover was higher at both sites above 23 degrees and sites below 21 degrees latitude compared to sites 21–23 degrees latitude, and shrub density was higher at sites below 21 degrees latitude than at sites 21–23 degrees latitude (Table 3.5). These results appear somewhat contradictory to those of the habitat type comparisons because there was no thorn forest at sites 21–23 degrees latitude. Thus, you would expect sites comprised mainly of deciduous and semi-deciduous habitats, and with no thorn forest, to have higher canopy cover and lower shrub density (see previous paragraph), yet the results suggest the opposite may be true. However, I consider these results a statistical artifact and not biologically meaningful. Within any vegetation type, there is considerable variability in the data for most parameters; the canopy cover values within the tropical deciduous forest sites (the predominant habitat type for sites 21–23 degrees latitude) generally were among the lower values, and the shrub density among the higher values, for that vegetation type across all sites. Thus, even though thorn forest generally has lower canopy cover and higher shrub density, in this case, the opposite appeared to be true for sites within the latitudes containing no thorn forest.

Although there were some differences between different groups as described above, the general pattern however was one of few differences between groups. There were no differences between groups based on elevation, differences among sex/age groups for only 1 of 7 variables, and differences among latitude groups for only 2 of 7 variables. The primary reason for the relative absence of differences among groups is the large variability (i.e., large SE relative to the means in Tables 3.4–3.8) for most variables across the comparisons. To make sure the large variability was not the product of uneven intervals, clustered data, or small sample sizes, I evaluated *post hoc* scatter plots of the data for all comparisons; the relative absence of breaks in the distributions suggests that the variability is real. Black-capped vireo occupancy across a broad range of values for most variables measured suggests they may have fewer restrictions in selecting winter habitat than they do for their breeding habitat, as was proposed by Graber (1961) and Gonzalez-Medina et al. (2009). More generally, the broad range of vegetation types in which black-capped vireos were found (e.g., thorn forest, tropical deciduous forest, tropical semi-deciduous forest, riparian gallery forest, mixed oak woodlands, pine-oak forest), including a range of disturbed and undisturbed forests, also suggests relatively relaxed winter habitat requirements.

Thus, the black-capped vireo is likely more of a habitat generalist species during the nonbreeding, winter season than it is during the breeding season. A more generalist strategy in habitat use among migratory birds during the winter season is not uncommon (reviewed by Rappole 1995). Niche theory predicts birds living in variable environments exhibit generalist and opportunistic strategies (Levins 1968, McNaughton

and Wolf 1970, Poulin et al. 1993), and the need to be more opportunistic may explain the broader spread in habitat characteristics during the arid dry season of western Mexico (Corcuera and Zavala-Hurtado 2006). Vega Rivera et al. (2010) suggested that the black-capped vireo's winter habitat is primarily tropical dry forest intermixed with a variety of other habitat types and ecotones. Additionally, they indicated that the vireo likely occurs in disturbed habitats only to the degree that those habitats are found within a broader matrix of forested areas, primarily tropical dry forest. My personal observations generally agree with this statement.

From a conservation perspective, the long-term persistence of black-capped vireos in their winter range may depend on the fate of the tropical dry forests they primarily occupy during the winter months. Vega Rivera et al. (2010) predicted that 64% of their winter distribution occurs in tropical dry forests. In this study, 54 of 56 (96.4%) sites occupied by black-capped vireos were found in tropical dry forest. Deforestation is the major threat for the long-term conservation of dry forests in western Mexico (Lugo 1988). Deforestation rates of dry forests in Mexico, estimated at 300,000 ha/year (2% per year) since the 1980s, are the highest among the different ecosystems in the country (Masera et al. 1997), making these forests one of the most endangered tropical ecosystems in the world (Janzen 1988, Murphy and Lugo 1995, Trejo and Dirzo 2000, Miles et al. 2006).

The extent of the transformation of Mexico's dry tropical forests has been large. By the early 1980s, 24% of the forest cover had been transformed for agricultural purposes, 20% for livestock grazing, and 9% for other purposes, leaving only 45% of the

forest cover intact (Toledo and Ordonez 1993). By the early 1990s, 73% of tropical dry forests in Mexico had been altered, degraded, or converted into agricultural or grazing lands, and only 27% of the original dry forests remained intact (Trejo and Dirzo 2000, 2002). Between 1990 and 2000, 36% of the remaining dry tropical forest was lost (Rickers et al. 2007). Most of the remaining primary tropical dry forest thus occurs in canyons, valleys, and ravines, where steep slopes inaccessible for agriculture serve as refuges for this forest type (Trejo and Dirzo 2000, Galicia et al. 2008). In light of this, it is probably not a coincidence that steep slopes were perhaps the most important predictor of black-capped vireo winter site occupancy.

Dry forest conversion has occurred in every state containing this vegetation type in Mexico, but some states may face more severe threats. For example, among the states with the largest remaining area of tropical dry forest (Sinaloa, Jalisco, Michoacán, Guerrero, and Oaxaca, in descending order; Cue-Bar et al. 2006), the most heavily impacted by anthropogenic conversion (measured as percent lost) are Jalisco (67.2%), Michoacán (65.7%), Oaxaca (55.9%), Guerrero (38.1%), and Sinaloa (36.0%; Toledo and Ordonez 1993). Thus, the relatively large tracts of remaining tropical dry forest that exist in Sinaloa (e.g., Trejo and Dirzo 2000, Cue-Bar et al. 2006, Rickers et al. 2007) may largely reflect the fact that conversion to agriculture, grazing, and other uses has been less intense in Sinaloa than in other states. Still, black-capped vireo habitat in Sinaloa is under heavy modification. Estimates indicate that 50% of native vegetation in Sinaloa has been modified for human activities (primarily agriculture and cattle grazing), with thorn scrub and tropical semi-deciduous forest habitats being most heavily

impacted (CONABIO 1999, Gonzalez-Medina et al. 2009, Leal-Sandoval et al. 2009). Of the land in Sinaloa that Vega Rivera et al. (2010) classified as potential black-capped vireo habitat, very little includes protected areas. This is a problem across the winter range of the vireo; Vega Rivera et al. (2010) stated that only about 7.1% of the predicted winter range under any form of protection, and most of that is protected in name only.

Jalisco has experienced the greatest losses of tropical dry forest. One unique factor at play in Jalisco that is adding an additional burden on the dry forests of the state has been the growth of the tequila industry, which is based upon the cultivation of agave (*Agave tequilana*) plants primarily grown in Jalisco. The tequila industry has experienced tremendous growth in the last 15-20 years, involving a large expansion of agave production into new areas within Jalisco (Macias Macias 2001, Bowen and Gerritsen 2007). For example, the amount of land in Jalisco dedicated to agave cultivation grew from less than 25,000 ha in 1998 to 163,000 ha by 2008 (Nunez et al. 2011) . The conversion of land for agave cultivation in Jalisco may help explain why I found relatively few vireos in this state compared to other nearby states. For example, correcting for survey effort (Table 2.1), I found 0.007 vireos/survey hour in Jalisco versus 0.04 vireos/hour in both Nayarit and Colima, and 0.04 vireos/hour in Sinaloa. Similarly, Vega Rivera et al. (2010) described how only one black-capped vireo was ever captured during intensive mistnetting and point-count surveys from 1999-2001 and from 2005-2008 at the Chamela Biological Station in Jalisco. Global demand for tequila will continue to increase the demand for agave cultivation in Jalisco, as will more recent efforts to use agave plants as a source of biofuel (Nunez et al. 2011).

The climate where tropical dry forests occur naturally is particularly suitable for livestock and agriculture, and human population densities are also higher in dry forest regions than in any of the world's other major tropical ecosystems (Murphy and Lugo 1986). Social, economic, and political forces in Mexico, like in many other developing countries, have placed additional pressures on the land (Barbier and Burgess 1996, Gerritsen 1998, Deininger and Minten 1999). Land transformation has been driven by perceptions and agro-pastoral policies that consider tropical forests as "wasted lands," only useful when transformed (SEMARNAT 2002, Castillo et al. 2005). Following the Second World War, government policies in Mexico's livestock and agricultural sectors led to incentives (e.g., subsidies for agricultural products, price control for basic crops, granting lands for new rural communities) to convert forest into agriculture and pasture fields (Barbier and Burgess 1996, Challenger 1998, Maass et al. 2005, Castillo et al. 2005). At the same time, the government initiated a program ("March to the Sea") to colonize the uninhabited and isolated coasts and to promote tourism by selling some of the territory to private entrepreneurs and by distributing other sections to landless and poor rural farmers (Castillo et al. 2005, Maass et al. 2005). Responding to these programs and incentives, most people began to arrive in the Pacific dry tropical forested areas during the 1960s and 1970s from other regions of Mexico, which led to the widespread transformation of these forests (Castillo et al. 2005, Galicia et al. 2008).

The main pattern of transformation of dry tropical forest involved clearing forests by completely removing vegetation, using slash and burn practices in the hillier landscapes and the use of machinery in the plains, to easily transform the forests into

agricultural (primarily maize, beans, or sorghum) and cattle pasture fields (Maass et al. 2005, Romero-Duque et al. 2007). After a few years, however, productivity declined because the shallow, rocky, and nutrient-poor soils found on the moderate to steep slopes of the region are not suitable for nutrient- and water-demanding agro-pastoral activities (Maass et al. 2005). Tenants then introduced non-native grasses and commenced cattle grazing (Burgos and Maass 2004).

In recent decades, national economic policies intended to liberalize the national economy have entailed the withdrawal of agricultural subsidies and credit incentives and, with declining corn prices, prompted the widespread abandonment of rural subsistence livelihoods in many areas (IMECBIO 1998, Galicia et al. 2008). Abandonment of unproductive lands promotes a landscape mosaic in which thorny plant communities and secondary forests, associated with the loss of native components, persist in the mid- and long-term (Rzedowski 1978, Burgos and Maass 2004). Secondary forests may have high ecological integrity because of the broad extent of area they occupy, the rapid regeneration of forest cover, and their importance in connectivity of landscape, refuges, and biological corridors (Galicia et al. 2008). Following abandonment of croplands, thorny woody vegetation dominated by *Acacia* and *Mimosa*, grow quickly and can cover the land after 5 years (Miller and Kauffman 1998, Burgos and Maass 2004). However, under intense alteration such as intense and prolonged overgrazing, these forests turn into ecologically stable plant associations that limit the regeneration of the original dry forest (Rzedowski and Calderon 1987, Eliason and Allen 1997, Trejo and Dirzo 2000).

Thus, the development of permanent pasture and agricultural plots consumes not only primary vegetation, but secondary vegetation as well, which may have serious conservation consequences for bird species that use early successional habitats (Petit et al. 1995). Early successional habitats are important for many migratory species (e.g., Lynch 1989, Blake and Loiselle 1992, Hutto 1992, Kricher and Davis 1992), which appear capable of using forested habitats in many stages of succession, especially in northern areas of the Neotropics (e.g., Lynch 1989, Hutto 1992, Petit et al. 1995). This may be true of black-capped vireos as well, in that they used a variety of vegetation types in this study, including areas with relatively open canopy and dense shrub layers which are indicative of early successional habitat. Hutto (1992) suggested that black-capped vireos are probably restricted to undisturbed tropical deciduous forest and unlikely to use second-growth habitat, but results from this study indicate otherwise. The conversion of primary forest for agricultural purposes across the wintering range of the black-capped vireo may create conditions suitable for winter use by vireos and other migrants, but intense and prolonged agricultural activities may ultimately degrade the capacity of those landscapes to provide long-term persistence of wintering avian communities. Vega Rivera et al. (2010) suggested that the value of disturbed habitats to the black-capped vireo may depend upon the degree to which those habitats are found within a broader forested matrix.

Land cover fragmentation occurs less frequently on mountainous areas than on low hills, where widespread agriculture (crops and grazing) is apparent and where human settlements are more likely to occur (Galicia et al. 2008). In mountainous areas,

land morphology increases slope vulnerability (landslides and soil erosion), limits accessibility (longer distance and topographically more challenging), and affects agricultural and residential development (Galicia et al. 2008). The highest degree and rate of deforestation occurs in the alluvial plain landforms found at lower altitudes by the coast, because availability of water, land, and accessible forests are conducive for human settlement and agricultural practices (Galicia et al. 2008). Thus, land clearing is more severe in the thorn forests typical of Mexico's Pacific coastal areas than it is in the steeper forests of higher altitudes (Dirzo 1994). Rohwer et al. (2009) stated that vast regions of coastal thorn forest have been converted to industrial agriculture in recent years across much of Sinaloa, and speculated that this may be responsible for concurrent declines in migratory species, such as the painted bunting (*Passerina ciris*) and the yellow-billed cuckoo (*Coccyzus americanus*).

The conversion of thorn forest to agriculture may be a threat to the black-capped vireo as well, considering their known occupancy of coastal thorn forest and evidence from this study that such habitat may be relatively more suitable for their occupancy than other habitats. Black-capped vireo winter habitat use was best predicted by increasing values of slope and foliage cover and decreasing values of canopy cover and tree DBH (model 11, Table 3.2; Fig. 3.2), and vireo plots classified as thorn forest habitat had greater foliage density, less canopy cover, and smaller tree DBH than other plots (Table 3.8). Therefore, it seems plausible that thorn forest provides more suitable conditions for vireo winter occupancy than do other vegetation types. Thus, the relative prevalence of vireos in tropical deciduous and semi-deciduous forests compared to thorn

forests in Sinaloa may have more to do with the less disturbed nature of the latter than it does a reflection of preference for the latter. Relatively large tracts of forest remain in the mountains of Sinaloa (e.g., Trejo and Dirzo 2000, Cue-Bar et al. 2006, Rickers et al. 2007), but widespread conversion of thorn forest near the coast (Rohwer et al. 2009, Rohwer 2013) may help explain why Gonzalez-Medina et al. (2009) found no black-capped vireos at any thorn forest sites and a larger concentration of vireos at a relatively pristine tropical deciduous forest site. More land within the elevation zones typical of tropical deciduous and semi-deciduous forest was predicted to be black-capped vireo habitat than was land within the lower elevation zones typical of thorn forest in recent ecological niche modeling studies. For example, Vega Rivera et al. (2010) predicted that 38% of vireo habitat was at elevations below 500m and Sarkar et al. (unpublished) predicted that 35% of vireo habitat was below 400m.

Nevertheless, all vegetation types in western Mexico have been heavily exploited to some degree, which is concerning from a conservation point of view. In addition to widespread conversion of the tropical dry forests, mixed oak woodlands and pine-oak forests have endured persistent threats as well. For example, Toledo and Ordonez (1993) described a loss of 55% of Mexico's tropical dry forests and 37% of its pine-oak forest and mixed oak woodlands. Gallery forests located along riparian areas also face heavy exploitation because the more fertile soils and availability of water in these areas makes them more appealing for agricultural practices and human settlement (Sanchez-Azofeifa et al. 2009). Additionally, very few protected areas exist across the winter range of the black-capped vireo. Vega Rivera et al. (2010) found that only 1.6% of land

within the predicted winter range of the black-capped vireo existed as a protected area (i.e., biosphere reserves, national parks, or wildlife protection areas), or 7.1% including some additional protected watersheds, although the authors caution that many of these areas are protected in name only. While more research is needed to understand the habitat use patterns of the black-capped vireo on its wintering grounds in Mexico, and the relative value of the different habitat types the species uses, it is clear that the future prospects for this endangered species will largely depend upon effective conservation of Mexico's forests.

CHAPTER IV

LINKING BLACK-CAPPED VIREO BREEDING GROUNDS AND WINTERING GROUNDS BY USE OF STABLE ISOTOPE ANALYSIS OF FEATHERS

Synopsis

Stable isotope signatures in animal tissues reflect those of local food webs, and tissues from animals that move between isotopically distinct food webs can retain information about previous feeding locations. Feathers are metabolically inert and therefore maintain an isotopic record reflecting the geographic location where the tissue was synthesized, which is on the breeding grounds for species like the black-capped vireo. In this study, I used stable isotopes in feathers (δ^2H, δ^{13}C, and δ^{15}N) to determine if feathers collected on the wintering grounds could be used to assess breeding origins and to determine if a relationship exists between breeding and wintering latitudes such as chain or leapfrog migration. I obtained feather samples from 144 black-capped vireos across 3 states in the breeding range and 8 states in the wintering range. All 3 isotopes analyzed in this study exhibited considerable within-state variability across the breeding and wintering grounds and did not provide sufficient information to establish migratory linkages between breeding and wintering sites. Multiple explanations for the observed variance from expectations are discussed. Future research should involve collecting and analyzing additional feathers across the breeding range, feathers from other resident birds, and testing groundwater for potential sources of influence on the data.

Introduction

In recent decades, several authors have documented declines in populations of some North American bird species (e.g., Robbins et al. 1989, Peterjohn et al. 1995, Sauer and Link 2011) and others have voiced concerns about the potential for further declines of Neotropical migrants (Terborgh 1989, Morton 1992, Terborgh 1992, Martin and Finch 1995, Faaborg et al. 2010). Much discussion has centered around whether this decline is due to factors occurring primarily on the breeding grounds (Whitcomb et al. 1981, Ambuel and Temple 1983, Holmes et al. 1986, Hutto 1988, Wilcove and Robinson 1990, Robinson 1992) or on the wintering grounds (Morse 1980, Askins et al. 1990, van der Have 1991, Rappole et al. 1992). Of course, factors occurring on both the breeding and wintering grounds may be impacting migratory birds, and the connectivity between events occurring in both locations may have important consequences for the ecology, evolution and conservation of Neotropical migratory birds (Myers et al. 1987, Sherry and Holmes 1995, Webster et al. 2002, Webster and Marra 2005, Faaborg et al. 2010).

Events in different stages of the annual life cycle of a bird can interact and influence subsequent events at the level of the individual and the population. Breeding densities are largely determined by winter survival, which, in turn is related to events that occurred during the previous breeding season (Fretwell 1972, Webster et al. 2002, Faaborg et al. 2010). Individual birds carry over effects between seasons, such as physical condition or date of arrival, that can explain important variation in reproductive success and annual survival (Gill et al. 2001, Harrison et al. 2011, Alves et al. 2013).

Winter habitat quality and food availability directly affect body condition of birds (Strong and Sherry 2000, Brown and Sherry 2006b), and body condition can indirectly affect reproductive success and survival (Peach et al. 1991, Marra et al. 1998, Sillett et al. 2000, Sherry et al. 2005). Winter habitat quality can influence timing of spring migration (Marra et al. 1998, Studds and Marra 2005, Rockwell et al. 2012), which may be important because individual migrants arriving early in temperate breeding areas appear to have higher reproductive success than do those arriving later (Lozano et al. 1996, Hasselquist 1998, Smith and Moore 2005, McKellar et al. 2013).

In order to understand how the biology of a species is influenced by the interactions of events on both the breeding and nonbreeding grounds, it is necessary to track populations or individuals between different phases of the life cycle. Efforts to track migratory songbirds with mark-recapture techniques or satellite telemetry are often ineffective (Hobson and Wassenaar 1999). An alternative approach that avoids many of the drawbacks of conventional tracking techniques involves stable isotope analysis of bird feathers. Isotopes are atoms whose nuclei contain the same number of protons but a different number of neutrons and thus have different atomic masses (Hoefs 2009).

Stable isotope signatures in animal tissues reflect those of local food webs, which in turn can vary spatially based on several biogeochemical processes, including temperature gradients, altitude, season, and distance inland from the coast (e.g., Peterson and Fry 1987, Tieszen and Boutton 1988, Bowen 2010). For example, stable hydrogen isotope ratios in precipitation show a latitudinal gradient in North America that is reflected in plants and subsequently animals that consume the plants (Hobson 1999,

2005, Bowen et al. 2005). Therefore, linkages between deuterium (δ^2H, an isotope of hydrogen) levels in local food webs and those in animals that feed at the same locations can be used to track migratory animals. Tissues from animals that move between isotopically distinct food webs can retain information about previous feeding locations.

Most species of Neotropical migratory songbirds grow feathers on or close to their breeding grounds before fall migration (Pyle 1997, Kelly et al. 2002). Feathers are metabolically inert and therefore maintain an isotopic record reflecting the geographic location where the tissue was synthesized (Mizutani et al. 1990). Therefore, tissue in a feather collected on the wintering grounds reflects the isotopic record during the breeding season (i.e., the period of growth), allowing researchers to effectively link these two areas (e.g., Hobson and Clark 1992). This relationship has been confirmed by recent investigation and the breeding origins of various wintering migrants subsequently have been determined based on this predictable relationship (e.g., Chamberlain et al. 1997, Wassenaar and Hobson 2000, Hobson et al. 2001, Rubinstein et al. 2002, Norris et al. 2006). Caution must be used in interpretation of stable isotopic patterns because there is evidence that altitude and distance from the coast may confound the results (Ziegler 1989, Graves et al. 2002, Marshall et al. 2007), although Kelly et al. (2002) found that these effects were not large enough to obscure the latitudinal pattern.

In addition to deuterium, other stable isotopes, such as those of carbon and nitrogen, can also reveal important information about the ecology of migratory birds. Plants differ in their isotopic signatures due to differences in photosynthetic pathway (e.g., C_3 vs. C_4 plants), nitrogen fixation process, soil moisture condition, and exposure

to nitrogen fertilizers (Rundel et al. 1989, Alisauskas and Hobson 1993, Bruggemann et al. 2011, Koehler et al. 2012). Since a latitudinal gradient exists in $\delta^{13}C$ values (relative to $\delta^{12}C$; Korner et al. 1991, Chamberlain et al. 1997) in North America, carbon isotope ratios in feathers collected on the wintering grounds should vary geographically according to their breeding sites. Nitrogen ($\delta^{15}N/\delta^{14}N$) isotope ratios are known to vary geographically in that they are generally more enriched in arid regions and depleted in wet regions (Koch et al. 1995, Reichlin et al. 2010), although there is local variation in nitrogen values as a function of site-specific nitrogen inputs (Kelly 2000). Although individual isotopes can reveal unique and valuable information about a species' migratory patterns, using several isotopes in combination may increase accuracy of assigning birds to their molting origins on the breeding grounds (Webster et al. 2002, Bell 2005, Sellick et al. 2009, Torres-Dowdall et al. 2009).

My overall goal for this research was to use recently developed techniques for measuring stable isotope ratios of elements in bird feathers to investigate the relationships between known breeding and wintering locations of black-capped vireos. Specific objectives for this research were to (1) determine if breeding latitude was related to stable hydrogen isotope ratio in black-capped vireo feathers, (2) determine if feathers collected on the wintering grounds could be used to assess the breeding origins of black-capped vireos, (3) and determine if a relationship exists between breeding and wintering latitudes (e.g., chain or leapfrog migration).

Methods

Study Location

Field research was conducted over 2 winter periods (31 January 2003–9 April 2003; 8 December 2003–19 March 2004) at study sites located along the Pacific slopes of the Sierra Madre Occidental mountains in western Mexico, and ranging in elevation from sea level to 1500 m (Fig. 2.1, Table 2.1). Sites were located in the states of Sinaloa, Durango, Nayarit, Jalisco, Colima, Guerrero, Michoacán, and Oaxaca.

The 3 broadly defined categories of forest within the Sierra Madre Occidental include thorn forest, tropical deciduous and semi-deciduous forest, and pine-oak forest (Miranda and Hernandez 1963, Rzedowski 1978, Ricker et al. 2007). Thorn forest grows in more arid regions at lower altitudes near the coast, whereas deciduous and semi-deciduous forests grow on the relatively more humid hills below the pine-oak woodlands, which occur at higher altitudes (Fig. 2.2; Arbingast et al. 1975).

Thorn forest, tropical deciduous forest, and tropical semi-deciduous forest all fall within the general classification of tropical dry forest. Mexico's tropical dry forests are found in dry to sub-humid climates (annual average rainfall 600-1200 mm) that are warm (annual average temperature 20-29 degrees Celsius) with highly marked seasonality (5- to 8-month dry season), and that occur at altitudes of 0-1500 m (Miranda and Hernandez 1963, Rzedowski 1978, Trejo 1999, Sanchez-Azofeifa et al. 2005). These forests are typically dominated by deciduous trees (more than 50%) and are predominantly established on moderate to steep slopes with shallow soils (Trejo and Dirzo 2002, Sanchez-Azofeifa et al. 2005).

Study sites included all 3 of the primary vegetation associations (i.e., thorn forest, tropical deciduous and semi-deciduous forest, and pine-oak forest) along the western slopes of the Sierra Madre Occidental. However, survey effort was not distributed equally among them because the relative areas of each vegetation association are not equal, access to each association is not equally reliable (e.g., road access is much easier at the lower elevations where human populations are found relative to higher elevation pine-oak forests), and vireos were not expected to occur equally among the vegetation associations. Most sites have been disturbed to some degree by human activities. Tropical dry forest frequently occurs in a mosaic of disturbed secondary vegetation and patches of relatively undisturbed primary vegetation (Trejo and Dirzo 2000, Gordon et al. 2004, Gove et al. 2005).

Data Collection

At study sites, I walked through scrub or forested habitats searching visually for individual black-capped vireos and also seeking auditory clues to their presence, including vocalizations by vireos and members of mixed-species flocks that sometimes associate with black-capped vireos. This approach has been used for winter studies of golden-cheeked warblers, another species in which winter vocalizations by the species are infrequent (e.g., Rappole et al. 1999, 2000). Upon finding focal black-capped vireos with visual and auditory surveys, birds were captured following standard protocol for mistnetting (Ralph et al. 1993). Black-capped vireos undergo a partial pre-alternate molt during the nonbreeding season in which a small percentage of birds replace 1 to 2 central

rectrices, but outer rectrices from the prebasic molt remain through the winter (Pyle 1997). Because my interest was in collecting feathers grown on the breeding grounds, I removed a single outer rectrix, as well as 2-3 breast feathers from each captured bird. I stored feathers from each bird in a separate paper envelope identifying the bird, date, location, and sex/age classification. Captured black-capped vireos were also banded with U.S. Fish & Wildlife Service metal bands. Prior to importation into the United States from Mexico, all feathers were immersed in 70% ethanol and then dried in order to meet U.S. Department of Agriculture border inspection requirements that the feathers are clean of blood, skin, and manure. The effects of ethanol on bird tissues have been demonstrated to have an insignificant effect on isotopic signatures (e.g., Hobson et al. 1997, Gloutney and Hobson 1998).

To supplement the feathers collected during my field investigations, I also obtained winter-season black-capped vireo feathers from museum collections (Appendix B). This allowed me to increase the overall sample size and expand the geographic coverage of my analysis because no vireos were observed (or feathers collected) during field investigations in the southern states of Michoacán, Guerrero, or Oaxaca. Vireo feathers collected from the wintering grounds were provided by the following institutions: American Museum of Natural History, British Museum of Natural History, Delaware Museum of Natural History, Field Museum of Natural History, Moore Laboratory of Zoology at Occidental College, Smithsonian Institution, University of California, Berkeley Museum of Vertebrate Zoology, and University of Kansas Natural History Museum.

In addition to feathers collected from the winter grounds, I also obtained feathers from black-capped vireos across a geographic gradient of the breeding range (including the Wichita Mountains in Oklahoma, Fort Hood in central Texas, and sites in Coahuila, Mexico). These were analyzed for comparisons of isotopic ratios between feathers grown in the breeding season and those collected from the winter grounds. Joe Grzybowski of the University of Central Oklahoma provided feathers collected from breeding populations at Fort Sill Military Reservation in Oklahoma, and David Cimprich of The Nature Conservancy, Fort Hood provided feathers collected from breeding populations at Fort Hood Military Reservation in central Texas. I obtained museum specimen feathers from breeding sites in Coahuila, Mexico that were provided by the following institutions: American Museum of Natural History, Field Museum of Natural History, University of California, Berkeley Museum of Vertebrate Zoology, and the University of Kansas Natural History Museum (Appendix B).

Data Analysis

Because the accuracy of assigning geographic origin of avian tissues increases with the number of different stable isotopes analyzed (Sellick et al. 2009, Torres-Dowdall et al. 2009), I examined 3 isotopes ($\delta^{2}H$, $\delta^{13}C$, and $\delta^{15}N$) in this study, similar to Wunder et al. (2005), Reichlin et al. (2010), and Hobson et al. (2012). All feathers collected were analyzed at the Colorado Plateau Stable Isotope Laboratory (CPSIL) in Flagstaff, Arizona. Prior to isotopic analysis, all feathers were cleaned of any surface contamination using a detergent solution and soaked in a 2:1 chloroform/methanol mixture to remove lipids (Hobson and Welch 1992), and then dried in a drying oven at

approximately 50º C for 48 hours. Segments were clipped from the vanes of each feather near the tip, pulverized with a mortar and pestle, encapsulated in either silver (δ^2H isotopes) or tin (δ^{13}C and δ^{15}N isotopes) capsules, and then weighed (0.33-0.37 mg for δ^2H and 0.60-1.20 mg for δ^{13}C /δ^{15}N) to the nearest ± 0.001 mg. Because each feather sample required two unique analyses (one for δ^2H and one for δ^{13}C /δ^{15}N) and because black-capped vireo feathers are small, there was not always sufficient tissue material in a sample to perform both analyses. In such cases, tissue was first selected for analysis of deuterium because it is more traditionally valuable for determining migratory origins. All samples were then analyzed via high-temperature pyrolysis using Finnigan Delta continuous flow isotope mass spectrometers that have been calibrated for specific isotopes (R. Doucett, pers. comm.). Samples analyzed for δ^{13}C and δ^{15}N were conducted simultaneously and samples analyzed for δ^2H were analyzed separately using a different instrument calibration.

Stable isotope abundances are expressed as the relative difference of a ratio of isotopes in a sample compared with that of a reference, typically an international standard, using the 'delta' (δ) notation (Werner and Brand 2001, Coplen 2011). The differences in ratios between the sample and standard are very small, and therefore expressed as parts per thousand or 'per mil' (‰) deviation from the standard. For example, for carbon:

$$\delta^{13}\text{Csample} = \{(^{13}\text{C}/^{12}\text{C sample}) / (^{13}\text{C}/^{12}\text{C standard}) - 1\} \times 1000$$

The standard is defined as 0‰ and for carbon, the international standard is Pee Dee Belemnite, a carbonate formation, whose generally accepted absolute ratio of ^{13}C/^{12}C is

0.0112372 (Colorado Plateau Stable Isotope Laboratory 2013). Materials with ratios of $^{13}C/^{12}C > 0.0112372$ have positive delta values, and those with ratios of $^{13}C/^{12}C < 0.0112372$ have negative delta values (Colorado Plateau Stable Isotope Laboratory 2013).

Hobson and Wassenaar published the first map of continental patterns of growing-season δ^2H based on the global network of precipitation sites database (i.e., the Global Network for Isotopes in Precipitation [GNIP]); Rozanski et al. 1992). Later, Meehan et al. (2004) modified this effort and published a high-resolution (1-km^2) model of North American stable hydrogen isotope ratios based on mean annual growing-season precipitation that accounts for the effect of elevation where previous models did not. Based on this map, Lott and Smith (2006) developed a map of expected feather deuterium values based on a large and geographically diverse sample of raptor feathers across North America, including northern Mexico (Fig. 4.1).

Today, it is possible to reliably estimate the δ^2H values of precipitation for different latitudes and longitudes using a spatially-explicit calculator (available at http://wateriso.utah.edu/waterisotopes/index.html; initially described in Bowen and Wilkinson 2002, Bowen and Revenaugh 2003). Using this calculator, I was able to predict expected deuterium values for the feather samples collected across the different sites of the black-capped vireo's breeding range. Black-capped vireos feathers collected on the breeding grounds in Oklahoma were expected to have deuterium values between -59 and -37‰, feathers collected in central Texas were expected to have deuterium values between -49 and -21‰, and feathers collected in Coahuila, Mexico were expected

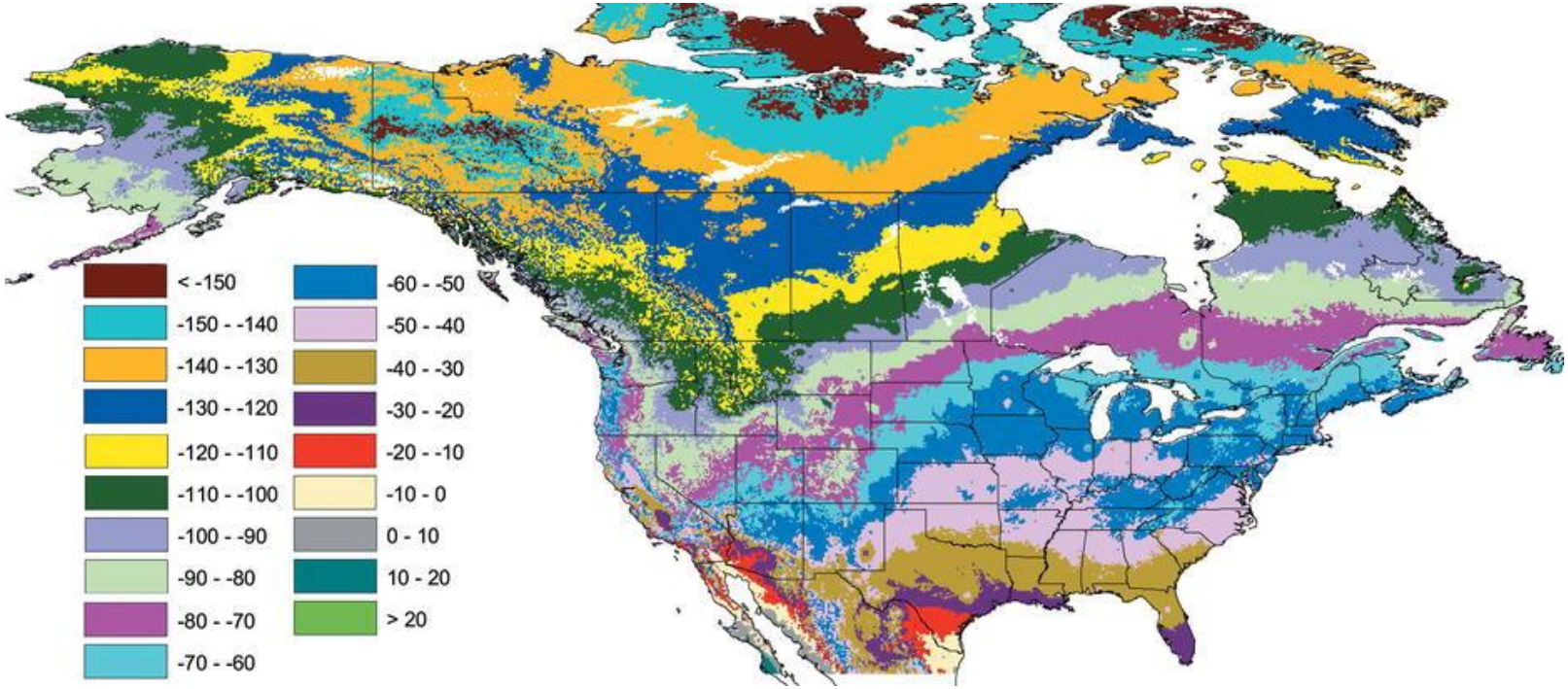

Figure 4.1. Map of deuterium (δ^2H) values (expressed as parts per thousand or ‰) for North American raptors (image courtesy of Lott and Smith 2007).

to have deuterium values between -70 and -24‰. For all feathers collected on the wintering grounds for which breeding origins are unknown, I expected deuterium values within the range predicted for breeding season feathers (i.e., between -70 and -21‰). The placement of individual winter season samples within distinct breeding regions (e.g., Oklahoma, Texas, Coahuila) based on deuterium values should provide insight into the migratory ecology of the black-capped vireo, such as evidence of either chain migration or leapfrog migration. Chain migration occurs where breeding populations move southward along the migration axis and retain the spatial relationship as in the breeding season, whereas leapfrog migration occurs where the winter distribution of breeding populations form a mirror image of their position in the breeding season (Bell 2005).

Korner et al. (1991) presented carbon isotope data for numerous plant species in temperate North America, and found a distinct latitudinal gradient. Based on the data in Korner et al. (1991) within the latitudes that represent the breeding range of the black-capped vireo (approximately 27-35°N), all black-capped vireos feathers were expected to have carbon-13 values between -28 and -24‰, with those grown towards the northern limits of the breeding range (i.e., Oklahoma) exhibiting the more depleted values. Nitrogen ($\delta^{15}N/\delta^{14}N$) isotope ratios are generally more enriched in arid regions and depleted in wet regions (Koch et al. 1995, Reichlin et al. 2010) and annual precipitation at the more eastern breeding locations (i.e., central Texas and Oklahoma) is generally twice that of the more western breeding locations (i.e., Coahuila; Western Regional Climate Center 2013). Therefore, black-capped vireo feathers grown in Oklahoma and

Texas were expected to have more depleted nitrogen isotope values than those grown in Coahuila. Annual precipitation in Comanche County, Oklahoma (the location of Fort Sill) is higher than in Bell County, Texas (the location of Fort Hood; Western Regional Climate Center 2013), so vireo feathers grown in Oklahoma were expected to have more depleted nitrogen isotope values than those grown in Texas.

To visually present the variation in the isotope data, I prepared box-and-whisker plots summarizing the data from each site of feather collection (for all breeding and wintering collection sites) for each isotope analyzed (δ^2H, δ^{13}C, and δ^{15}N). I also plotted deuterium (δ^2H) isotope ratios of black-capped vireo feathers collected from the breeding and wintering grounds against the latitude at which the feathers were collected and fit a linear regression line to the data. There should be a positive relationship between the latitude of breeding samples and the stable hydrogen isotope ratio because the location of feather growth is known for samples collected on the breeding grounds and that relationship has been confirmed for many species in numerous studies. If there is a positive relationship between the latitude of winter collection sites and the stable hydrogen isotope ratio, this would suggest evidence of leapfrog migration whereby the birds that breed at the northern limits of the breeding range wintered at the southern limits of the winter range (e.g., Kelly et al. 2002). A negative relationship between latitude of winter collection sites and the stable hydrogen isotope ratio would indicate evidence of chain migration. If neither a positive nor a negative relationship between latitude of winter collection sites and stable hydrogen isotope ratios is found, this would suggest a potentially more complex migration system for the species. Because there is

also a potential latitudinal gradient for carbon, I also plotted carbon ($\delta^{13}C$) isotope ratios of black-capped vireo feathers collected from the breeding and wintering grounds against the latitude at which the feathers were collected and fit a linear regression line to the data.

I tested for differences in deuterium isotope values among groups of feather samples categorized by latitude using the Mann-Whitney *U* test. This included testing for differences in deuterium values among the three distinct breeding latitudes (e.g., samples from Oklahoma vs. Texas, Oklahoma vs. Coahuila, and Texas vs. Coahuila), and also testing for differences among different wintering latitudes (i.e., I ranked the winter samples by latitude then tested for differences between values from samples north of the median latitude vs. those south of the median latitude). I also tested for differences in nitrogen isotope values among the three distinct breeding locations using the Mann-Whitney *U* test.

Results

I obtained feather samples from 144 black-capped vireos for isotopic analysis, including 64 from the winter grounds and 80 from the breeding grounds (Table 4.1; Appendix B). Winter-range feather samples used in the analyses (26 of which I collected in the field, and 38 of which were provided by museums) included 17 from Sinaloa, 5 from Durango, 25 from Nayarit, 5 from Jalisco, 8 from Colima, 1 from Michoacán, 1 from Guerrero, and 2 from Oaxaca. Breeding-range feather samples used in the analyses included 20 collected at Fort Sill Military Reservation in Oklahoma, 46

Table 4.1. Summary of black-capped vireo feathers used in stable isotope analyses, including locations where feathers were collected, and if feathers were acquired from field investigations or specimen tissues provided by museum collections.

Location[1]	Field[2]	Museum	Total
Breeding			
OKL	20	0	20
TEX	46	0	46
COA	0	14	14
Wintering			
SIN	6	11	17
DUR	1	4	5
NAY	13	12	25
JAL	1	4	5
COL	5	3	8
MIC	0	1	1
GUE	0	1	1
OAX	0	2	2
Total	92	52	144

[1] Feathers collected from breeding sites include the 3 primary states of breeding occupancy: Oklahoma (OKL), Texas (TEX), and Coahuila, Mexico (COA). Feathers collected from wintering sites include the 8 Mexican states of known winter occupancy: Sinaloa (SIN), Durango (DUR), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacán (MIC), Guerrero (GUE), and Oaxaca (OAX).

[2] Joe Grzybowski provided all feathers collected in the field from Oklahoma (Fort Sill Military Reservation, Comanche County); David Cimprich provided all feathers collected in the field from Texas (Fort Hood Military Reservation, Bell and Coryell Counties); I collected all feathers collected across sites in the winter range in Mexico.

collected at Fort Hood Military Reservation in central Texas, and 14 provided by museums from Coahuila, Mexico. Sample sizes for isotopic studies were different for deuterium (142 samples) and for carbon/nitrogen (119 samples) because I prioritized deuterium analyses when tissue material was of insufficient quantity to run both analyses, and because some individual samples were discarded during laboratory analysis due to errors.

Deuterium (δ^2H) values showed considerable variability for all collection sites on the breeding and wintering grounds for which there were sufficient sample sizes to exhibit variability (Fig. 4.2). The relationship between deuterium values and latitude of collection site was not significant for feathers collected on the breeding grounds ($y= -0.9393x -29.256$; $R^2= 0.0076$; $P= 0.45$; Fig. 4.3) or the wintering grounds ($y= -0.4452x - 57.176$; $R^2= 0.0043$, $P= 0.57$; Fig. 4.4).

Among samples collected across the breeding grounds, feather deuterium values differed significantly between Oklahoma and Coahuila (Mann-Whitney $U=67$, $P\leq 0.05$, $n_1=20$, $n_2=13$, two-tailed) and between Texas and Coahuila ($U=442.5$, $P\leq 0.05$, $n_1=44$, $n_2=13$, two-tailed), but not between Oklahoma and Texas ($U=540$, $P>0.05$, $n_1=44$, $n_2=20$, two-tailed). Feather deuterium values did not differ significantly between samples collected in the northern half of winter sites and those collected in the southern half of winter sites ($U=762.5$, $P>0.05$, $n_1=n_2=39$, two-tailed).

Deuterium values for all collection sites did not closely match expected values at some sites (Table 4.2). The mean value for samples from Texas fell outside of the expected range of values, and 61%, 50%, and 23% of samples for Texas, Oklahoma, and

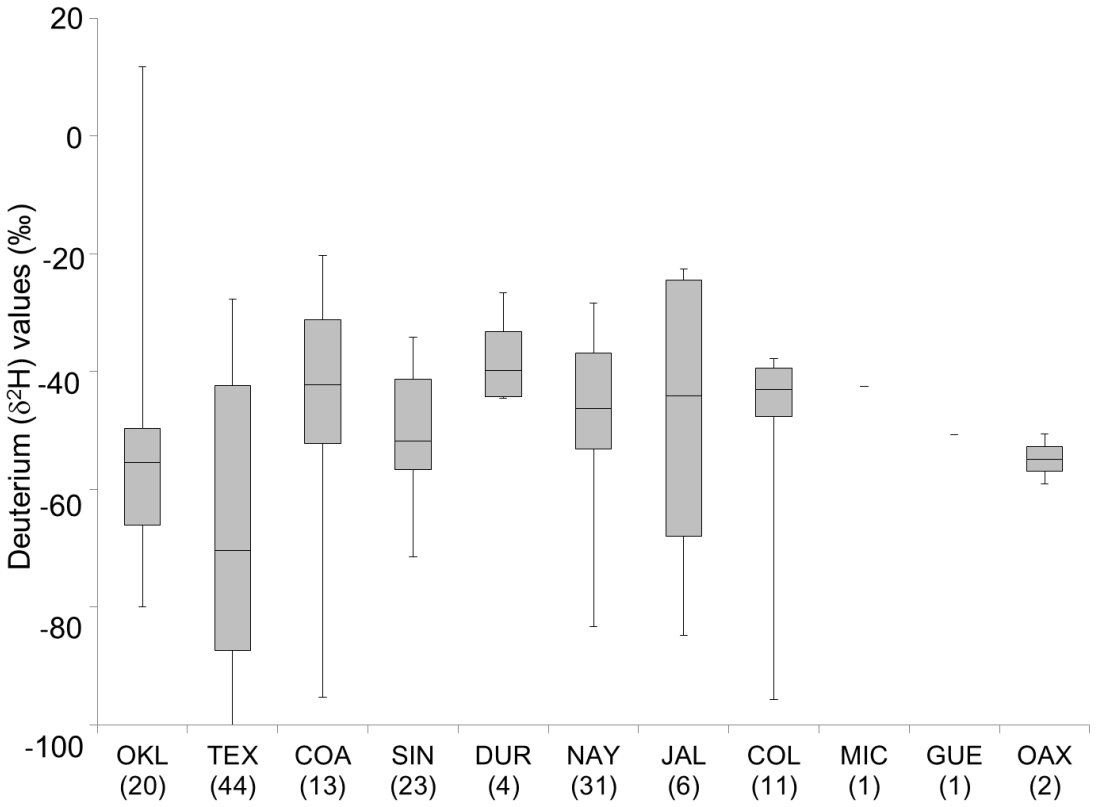

Figure 4.2. Box-and-whisker plot of deuterium (δ^2H) values (expressed as parts per thousand or ‰) for black-capped vireo feathers collected on the breeding and wintering grounds. States representing the breeding grounds include Oklahoma (OKL), Texas (TEX), and Coahuila (COA), and states representing the wintering grounds include Sinaloa (SIN), Durango (DUR), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacán (MIC), Guerrero (GUE), and Oaxaca (OAX). Sample sizes appear in parentheses beneath each state along the x-axis. The middle 50% of the data lies within the shaded box in each column, with the median value represented by a horizontal line. Whiskers extending above and below the box represent the maximum and minimum values, respectively.

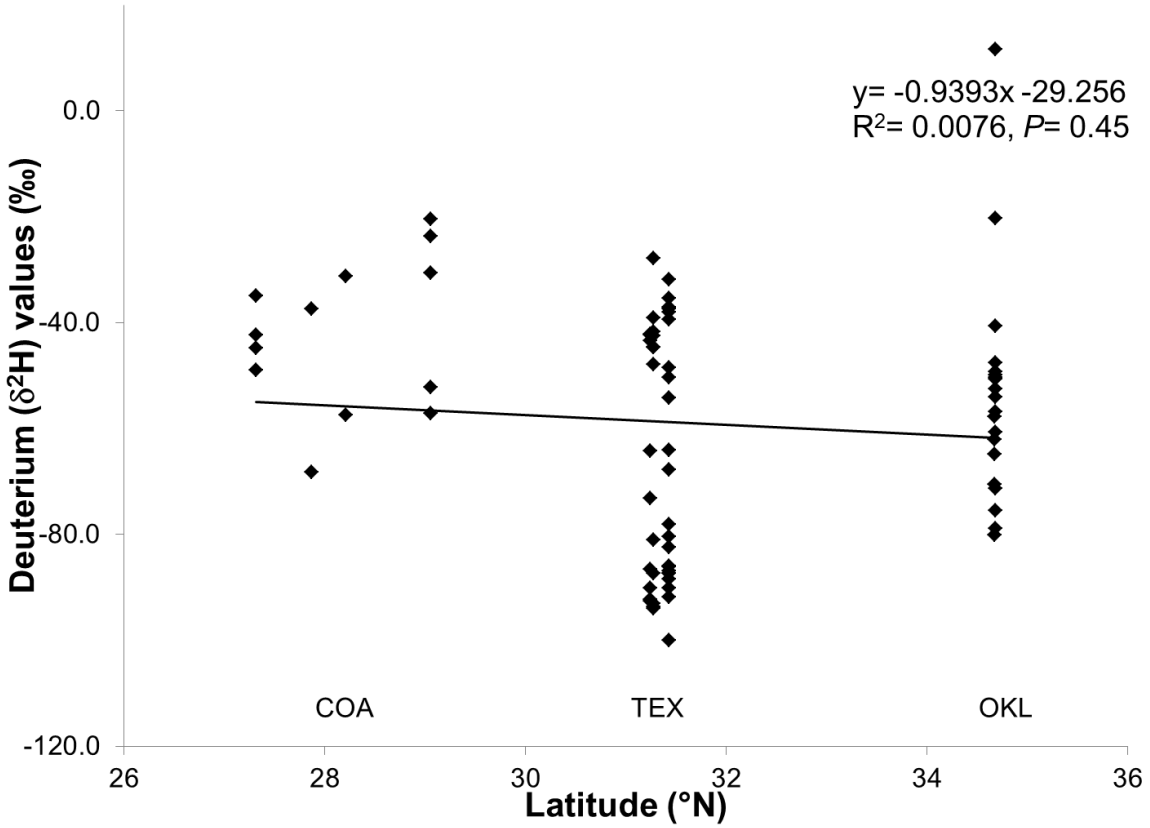

Figure 4.3. Deuterium (δ^2H) isotope ratios of black-capped vireo feathers collected from the breeding grounds plotted against the latitude at which the feathers were collected. Breeding season feathers were collected from sites in Coahuila, Mexico (COA), Fort Hood Military Reservation in central Texas (TEX), and Fort Sill Military Reservation in Oklahoma (OKL), as labeled above the x-axis. The slope and intercept of the regression line, the R-squared value, and the p-value in the upper right corner of the figure.

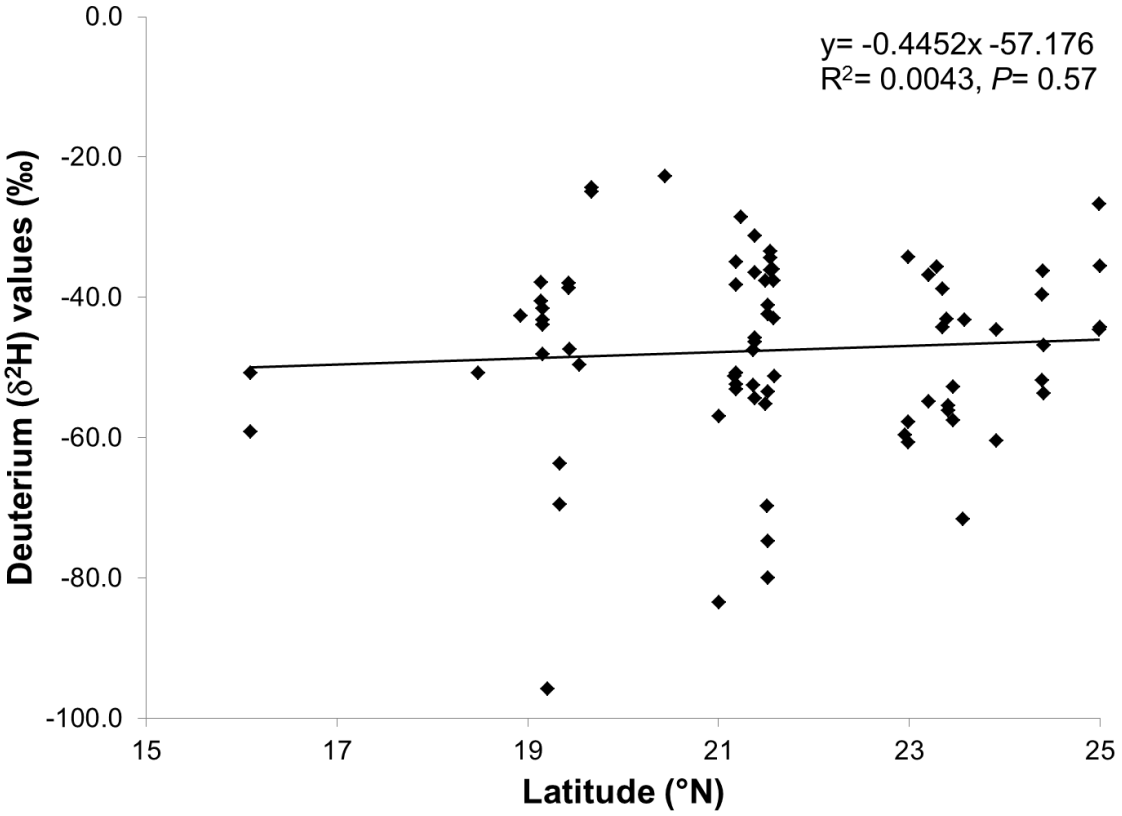

Figure 4.4. Deuterium (δ^2H) isotope ratios of black-capped vireo feathers collected from the wintering grounds plotted against the latitude at which the feathers were collected. Winter season feathers were collected from the Mexican states of Oaxaca, Guerrero, Michoacán, Colima, Jalisco, Nayarit, Durango, and Sinaloa, representing a gradient of lower to higher latitudes. The slope and intercept of the regression line, the R-squared value, and the p-value are presented in the upper right corner of the figure.

Table 4.2. Comparison of expected vs. actual deuterium isotope values for black-capped vireo breeding locations in Oklahoma, Texas, and Coahuila. The range of expected values is based on the calculator using Global Network of Isotopes in Precipitation (GNIP) data, geographic coordinates, and elevation.

Location	n	Expected Range	Actual Range	Actual Mean	% Outside of Expected Range
Oklahoma	20	-59 to -37	-80 to +11	-54.1	50%
Texas	44	-49 to -21	-100 to -28	-66.2	61%
Coahuila	13	-70 to -24	-95 to -20	-45.2	23%

Coahuila, respectively, also fell outside of the expected range of values (Table 4.2). However, only 7.5% of all samples collected on the wintering grounds fell outside of the expected range of values for the entire breeding range (i.e., -70 to -24‰).

Carbon ($\delta^{13}C$; Fig. 4.5) and nitrogen ($\delta^{15}N$; Fig. 4.6) values showed considerable variability for all collection sites on the breeding and wintering grounds for which there were sufficient sample sizes to exhibit variability. There was a significant negative relationship between latitude of collection site of breeding ground feathers and carbon isotope values ($y= -0.3919x -10.227$; $R^2= 0.2376$; $P<0.001$; Fig. 4.7). The carbon isotope values did not closely match the expected values based on data in Korner et al. (1991), as the mean carbon isotope value for all samples (-21.9‰), the mean value for each individual state, and 86% of all samples were more enriched (i.e., less negative) than the expected range of values (i.e, between -28 and -24‰).

As predicted, nitrogen isotope values were more depleted among feather samples collected in Oklahoma (mean= 5.3‰) than in Texas (6.7‰), and nitrogen isotopes were more depleted in both Oklahoma and Texas than in Coahuila (7.2‰). These relationships were significant for Oklahoma vs. Texas ($U=119$, $P<0.05$, $n_1=38$, $n_2=11$) and Oklahoma vs. Coahuila ($U=34$, $P<0.01$, $n_1=14$, $n_2=11$), but not for Texas vs. Coahuila ($U=252.5$, $P>0.05$, $n_1=38$, $n_2=14$, all two-tailed). However, matching samples collected from the wintering grounds with those from the breeding grounds based on nitrogen isotopes is difficult because mean nitrogen values from 5 of the 8 wintering states were more enriched than for all of the breeding states (i.e., mean= 7.2‰ in

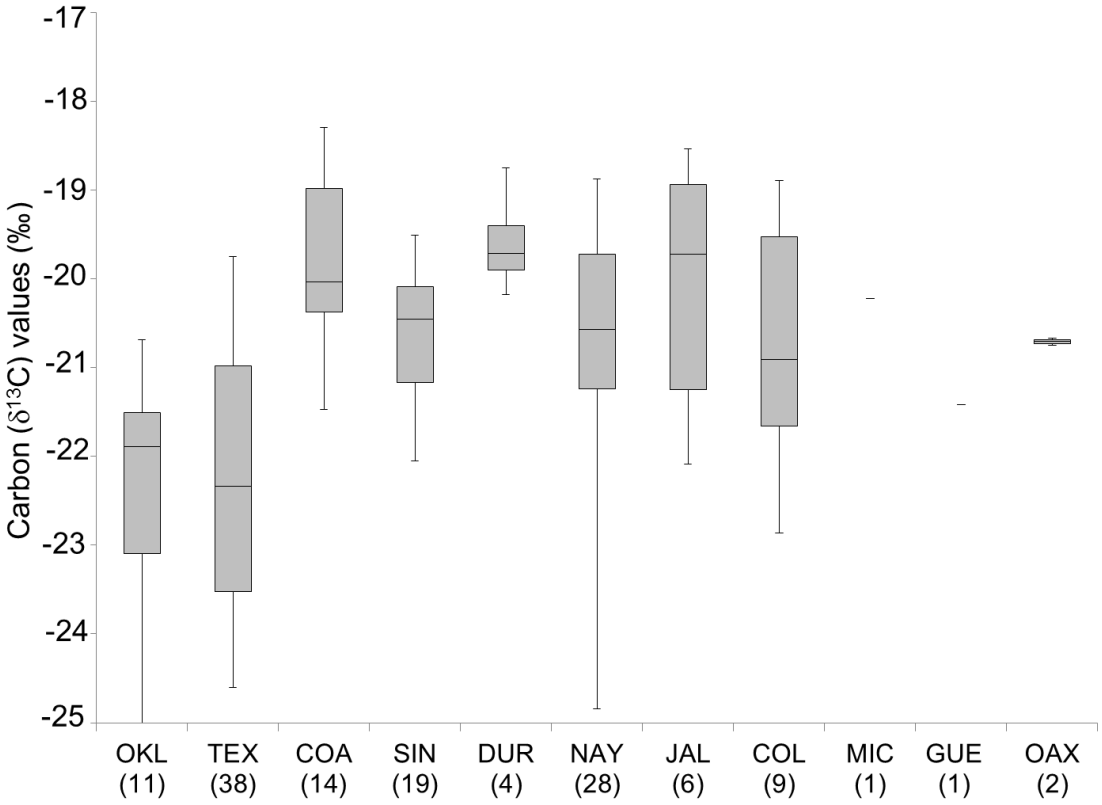

Figure 4.5. Box-and-whisker plot of carbon (δ^{13}C) values (expressed as parts per thousand or ‰) for black-capped vireo feathers collected on the breeding and wintering grounds. States representing the breeding grounds include Oklahoma (OKL), Texas (TEX), and Coahuila (COA), and states representing the wintering grounds include Sinaloa (SIN), Durango (DUR), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacán (MIC), Guerrero (GUE), and Oaxaca (OAX). Sample sizes appear in parentheses beneath each state along the x-axis. The middle 50% of the data lies within the shaded box in each column, with the median value represented by a horizontal line. Whiskers extending above and below the box represent the maximum and minimum values, respectively.

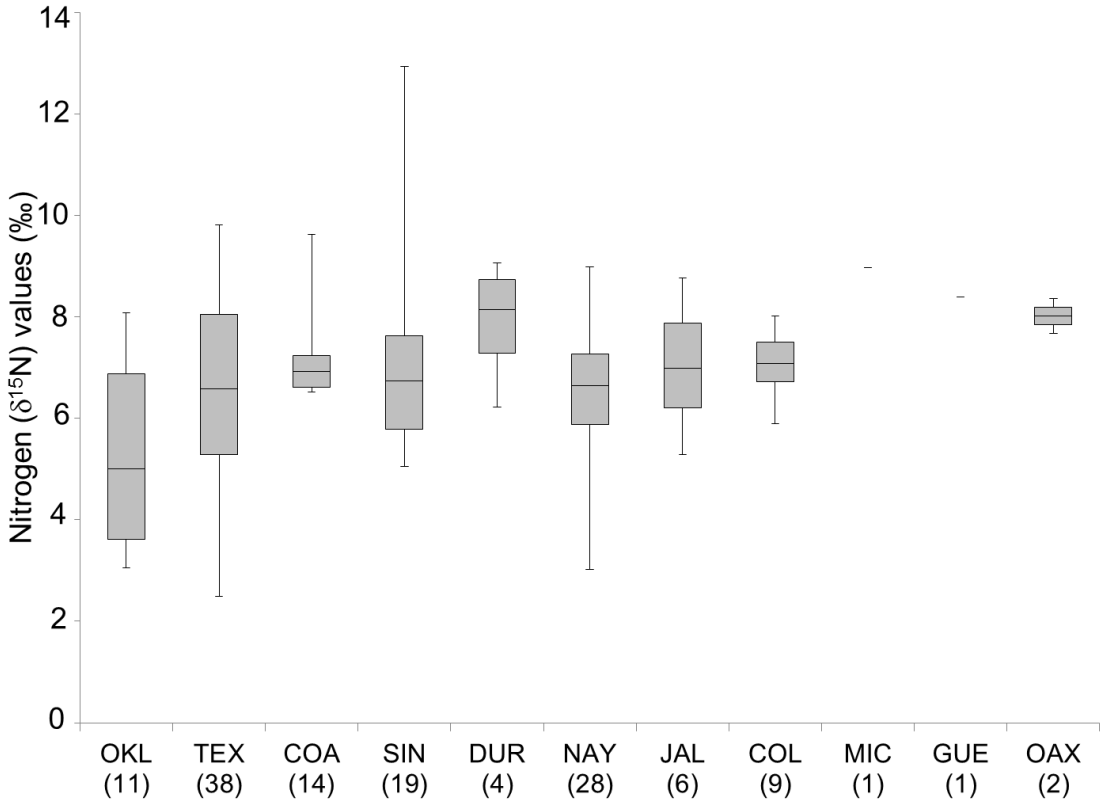

Figure 4.6. Box-and-whisker plot of nitrogen ($\delta^{15}N$) values (expressed as parts per thousand or ‰) for black-capped vireo feathers collected on the breeding and wintering grounds. States representing the breeding grounds include Oklahoma (OKL), Texas (TEX), and Coahuila (COA), and states representing the wintering grounds include Sinaloa (SIN), Durango (DUR), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacán (MIC), Guerrero (GUE), and Oaxaca (OAX). Sample sizes appear in parentheses beneath each state along the x-axis. The middle 50% of the data lies within the shaded box in each column, with the median value represented by a horizontal line. Whiskers extending above and below the box represent the maximum and minimum values, respectively.

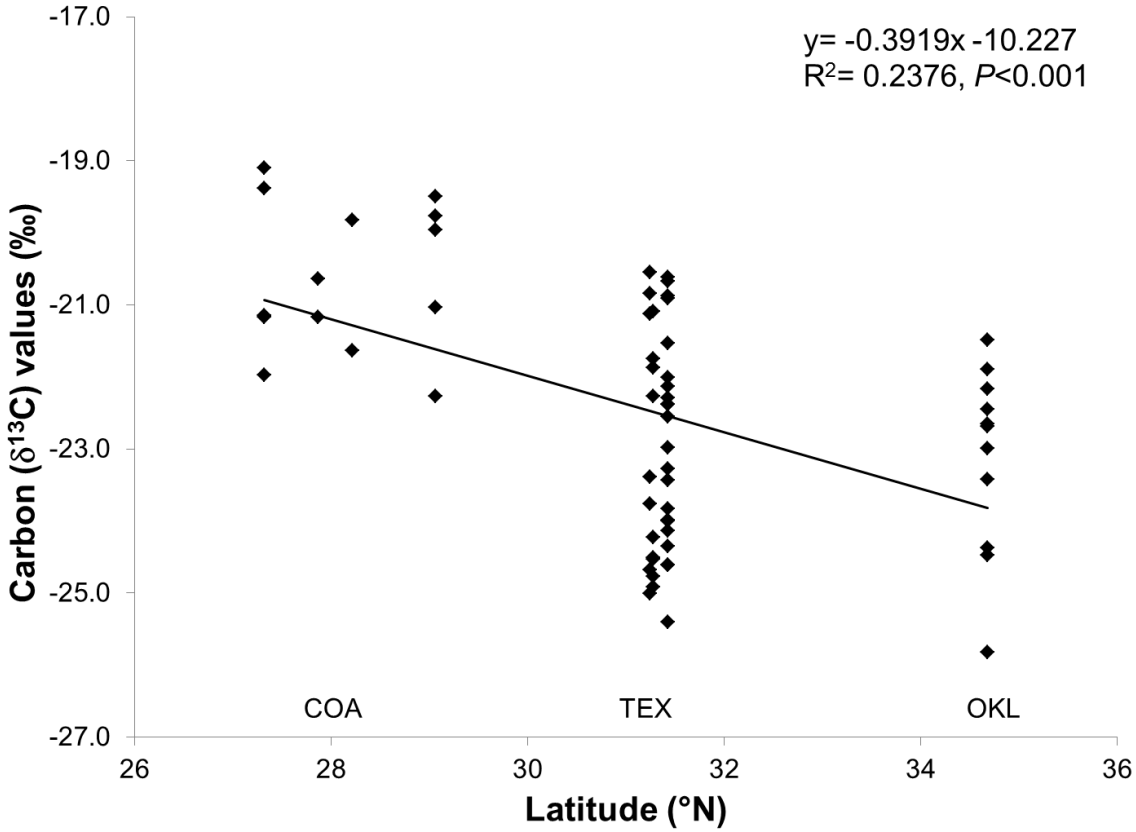

Figure 4.7. Carbon ($\delta^{13}C$) isotope ratios of black-capped vireo feathers collected from the breeding grounds plotted against the latitude at which the feathers were collected. Breeding season feathers were collected from sites in Coahuila, Mexico (COA), Fort Hood Military Reservation in central Texas (TEX), and Fort Sill Military Reservation in Oklahoma (OKL), as labeled above the x-axis. The slope and intercept of the regression line, the R-squared value, and the p-value are presented in the upper right corner of the figure.

Sinaloa, 7.9‰ in Durango, 6.4‰ in Nayarit, 7.0‰ in Jalisco, 7.0‰ in Colima, 9.0‰ in Michoacán, 8.4‰ in Guerrero, and 8.0‰ in Oaxaca).

Discussion

All 3 isotopes analyzed in this study exhibited considerable within-state variability across the breeding and wintering grounds. Even for sites where samples were collected in the same location within a single year or two years (e.g., Fort Sill in Oklahoma and Fort Sill in Texas), there still was considerable variability in the data, which does not fit with expectations from previous studies or with an understanding of how isotopes typically function in ecological systems. Additionally, there was not much agreement between expected and actual relationships between isotope values of vireo feathers and latitude of collection sites across the breeding grounds. For example, I did not find a significant relationship between δ^2H values and latitude of breeding sites (Fig. 4.3, Table 4.2). It is difficult to try to link wintering sites with breeding sites based on δ^2H values from feathers collected in this study when the values for the breeding sites do not tightly correspond with expected values. While I could ignore the isotope data collected from the breeding grounds and try to place results from winter samples with expected patterns across the breeding grounds using precipitation patterns, it is still difficult to know whether the winter feathers are reliable without knowing why the breeding ground feathers are not reliable.

There was a significant relationship, as expected, between δ^{13}C values and latitude of breeding sites (Fig. 4.7), and nitrogen isotope ratios were significantly more

enriched in the more arid regions of Coahuila than in Oklahoma or Texas as expected, but both $\delta^{13}C$ and $\delta^{15}N$ values were generally more enriched than expected at most sites. Correspondingly, $\delta^{2}H$ values were generally more depleted than expected at many sites, particularly for samples collected in Texas. For all 3 isotopes measured in this study, results not closely matching expectations suggest that caution is warranted in interpreting any results that were significant.

There was a weak but positive relationship between $\delta^{2}H$ and latitude for wintering sites, which would be interesting if significant because it would suggest the occurrence of leapfrog migration where the birds that bred at the northern limits of the breeding range wintered at the southern limits of the winter range and vice versa. However, I found no significant relationship in $\delta^{2}H$ values between the northern and southern halves of feathers collected on the wintering grounds, which suggests no discernible difference in their breeding origins. Furthermore, a problem with linking feathers collected from winter locations with specific breeding sites using $\delta^{2}H$ isotopes is difficult because the range of expected $\delta^{2}H$ values for Coahuila (i.e., -70 to -24‰) is broad enough that it almost completely encompasses the range of expected values from Texas (-59 to -37‰) and Oklahoma (-49 to -21‰). There is some overlap in values between Texas and Oklahoma, but still enough of a difference that some placement of winter feathers into breeding ranges might be possible, except that almost all values that could be fit into one of these two ranges of values also fits into the broad range of expected values from Coahuila. The large range of expected values in Coahuila likely results from the high and varied altitudes of the region. Higher altitudes produce more

depleted δ^2H values (Peterson and Fry 1987, Tieszen and Boutton 1988), and the feather samples from Coahuila used in this study were collected across a range of altitudes. If the sites in Coahuila were at lower altitude sites, such as those in Texas and Oklahoma, some useful discrimination between data across the 3 breeding locations may have been possible.

There are a number of possible explanations for why results from my samples differed from what was expected. First, instrumentation failure at the laboratory performing the isotopic analyses could have produced unreliable data. This is unlikely because the CPSIL, where the analyses were performed, processes all samples alongside a series of other materials that are used for quality assurance and quality control. These standards have known isotope values and upon completion of each analysis, they are evaluated for consistency with known values. If the results for the standards meet expectations, then the equipment was performing properly and all of the samples were accurately analyzed. This was the case with my samples; the spreadsheets I received from the laboratory with the results of the analysis include the standards, all of which met expectations. The lab manager (R. Doucett) later confirmed the rigor of the analysis as well.

Second, the immersion of all feathers in 70% ethanol prior to importation into the United States from Mexico may have affected isotopic composition of the feathers. Some evidence suggests ethanol can alter isotopic signatures in animal tissues (e.g., Vizza et al. 2013), although others have reported this effect to be insignificant (e.g., Hobson et al. 1997, Gloutney and Hobson 1998). Even if ethanol was a factor, this

would have only affected the feather samples I collected on the wintering grounds, not any feathers collected across the breeding range or provided by museums. The data that most poorly matched expected values came from breeding ground feathers, which could not have resulted from the application of ethanol.

Third, evapotranspiration within xeric environments can result in isotopic enrichment within the local food web (e.g., Kurz-Besson et al. 2006). Because conditions across much of the breeding range of the black-capped vireo are dry, particularly during the late summer period when vireos are molting their feathers, isotopic enrichment due to evapotranspiration could potentially explain aberrant patterns in my results. However, my samples are not unusually enriched, but unusually depleted in δ^2H, so this explanation is not likely a factor.

Fourth, animals occupying different biomes with different photosynthetic pathways (e.g., C_3, C_4, Crassulacean acid metabolism [CAM]) are exposed to food webs differing in isotope abundance (Hobson et al. 2010). If plants having CAM play a significant role in the ecosystem, they may increase variability due to the more enriched δ^2H values of these plants compared with C_3 or C_4 plants (e.g., Sternberg et al. 1984, Sternberg 1989). However, most CAM plants are either epiphytes (e.g., orchids, bromeliads) or succulent xerophytes (e.g., cacti, agaves) that occur in desert environments, although some CAM plants are wetland plants. None of these typically occur within the known breeding habitats of the vireo, so the influence of CAM plants is not a likely explanation for the δ^2H values found in vireo feather samples.

Fifth, the source water driving the local food webs used by breeding black-capped vireos could be from river systems that derive from more northern regions or from high altitude snowmelt. It is well established that δ^2H values are more depleted at higher latitudes and higher altitudes in North America (e.g., Peterson and Fry 1987, Tieszen and Boutton 1988), thus if vireo breeding habitats received input from high-latitude or altitude water, this might explain the depleted δ^2H values found in this study. However, this is unlikely to be the case for vireos in either central Texas or in Oklahoma, both of which are hundreds of miles from high altitude or high latitude regions and neither of which receives water from any riverine system. The influence of high latitudes could possibly explain depleted values collected on wintering grounds if those individual vireos molted at breeding sites in higher-altitude regions of northern Mexico, but this does not explain depleted values from samples collected in Oklahoma or the particularly depleted samples from Texas.

Sixth, local habitats used by vireos may be driven by groundwater that is decoupled from isotopic predictions based on the precipitation-based GNIP database. Groundwater from underlying aquifers within the vireo's breeding range could influence δ^2H patterns within the local food webs. Musgrove and Banner (1993) discovered extremely negative deuterium values (as low as -108‰) in spring water at sites around the border of Missouri and Oklahoma resulting from mixing of water in the underlying aquifers with water from mountainous areas in Colorado and passing through the Permian salt deposits in Kansas. It is unknown if or how the underlying aquifers at vireo feather collection sites in central Texas and Oklahoma may influence the negative

isotope values observed in this study. To better understand this, future research should aim to better understand the hydrology of these sites and whether groundwater may be getting into the food web and skewing the δ^2H values. Additionally, efforts to collect and isotopically analyze both groundwater samples and feather samples from resident birds at these sites would be useful to compare against the vireo feather data from this study.

Interestingly, Hobson et al. (2012) collected 544 feather samples from locations across North America and the only sample they eliminated as an outlier for being too depleted (δ^2H= -81.7‰) came from Williamson County, Texas, which is known to be occupied by black-capped vireos and is close to Fort Hood where my samples were collected. The authors argued that the depleted sample likely derived from a food web altered by irrigation from the Colorado River. Their explanation for depleted samples in Williamson County is not likely true of the depleted samples in this study because the Colorado River does not run near Fort Hood, but it is possible that some other sort of local phenomenon around Fort Hood is at play here, or that some larger regional pattern affecting the food webs explains both the depleted samples from Fort Hood and the depleted sample from nearby Williamson County documented by Hobson et al. (2012).

Seventh, as much as the deuterium isoscape for North America has been a valuable tool for many ecological studies such as those tracing migratory origins of birds (e.g., Chamberlain et al. 1997, Wassenaar and Hobson 2000, Hobson et al. 2001, Rubinstein et al. 2002, Norris et al. 2006), it is not well suited to highly pulsed systems (i.e., marked by intense, infrequent precipitation; K. Hobson, pers. comm.). Indeed,

most published studies using isotopes to link breeding and wintering sites of birds have focused on birds in eastern North America, a region where rainfall patterns are typically less variable. In eastern North America, there is a strong correlation between the measured feather isotope values of birds at sites and the predicted growing-season average precipitation value for the sites. However, if the precipitation that drives a food web used by birds is actually pulsed by a few key months of rainfall that are not necessarily typical of the whole year, such as in xeric environments, then departures from the expected pattern may occur.

Not only are pulses of rainfall a potential factor explaining unusually depleted δ^2H values in local food webs, but the directional origins of the air mass that produces the rainfall may also play a role. Air masses arriving at a given location via different circulation trajectories often carry moisture with very different isotopic composition (Liu et al. 2010), so the origins of rain fronts may play a factor in subsequent isotopic patterns in food webs. For example, Friedman et al. (2002) found significant differences in the δ^2H values of moisture reaching the Great Basin via transport from the North Pacific, subtropical Pacific, Gulf of California, and Gulf of Mexico, with lower values corresponding to precipitation events derived from the more northerly sources.

Monsoonal rains during or just prior to the period of molt by birds may drive a late primary production peak that ultimately was used by molting birds. In general, the deuterium content of precipitation decreases with increasing amounts of precipitation (Ziegler 1989), so uncharacteristically high rainfall during the summer during or prior to feather molt by black-capped vireos on the breeding grounds in Texas may have resulted

in the birds feeding on a fairly negative food web, contributing to unexpectedly depleted feather δ^2H values.

To examine this possibility, I looked at rainfall patterns at weather stations near Killeen and Fort Hood, Texas during the summers of feather collection (2003 and 2004) and compared them against normal 30-year average precipitation patterns for the area. Black-capped vireo feather molt at Fort Hood begins in late June or early July and continues into August (Butler et al. 2008), so I examined monthly June-August precipitation data from the 5 closest sampling stations (all in Bell County) and compared against 30-year averages for Killeen in Bell County and Gatesville in Coryell County, representing the southern and northern edges of Fort Hood. The 30-year average June rainfall is 94 mm in both Killeen and Gatesville (Texas State Climatologist 2013), but the average June rainfall across the 5 nearest sampling stations was 155 mm in 2003 and 279 mm in 2004 (NOAA National Climatic Data Center 2013), an increase of 65% and 197%, respectively, in June rainfall over the normal. The July 30-year average rainfall is 46 mm in Killeen and 61 mm in Gatesville, while rainfall during 2003 was 30 mm at both locations; the August 30-year average rainfall is 56 mm in Killeen and 64 mm in Gatesville, while rainfall was 43 mm during 2003 and 104 mm during 2004 (NOAA National Climatic Data Center 2013, Texas State Climatologist 2013). The significant increases in rainfall during June of each year, particularly in 2004, stand out from these data. Because black-capped vireos at Fort Hood begin molt during June, it is possible that the high rainfall in June of 2003 and 2004 brought uncharacteristically depleted

deuterium into the local food web at the time the vireos were starting to molt, affecting the results from this study.

Eighth, unexpectedly depleted feather δ^2H values may result if the black-capped vireo actually molts at higher altitudes than the assumed location at breeding locations in Texas and Oklahoma. This could be the case if the vireos departed their breeding grounds prior to molting and moved to the Mexican monsoon region (Douglas et al. 1993), which coincides with their winter grounds and experiences a large increase in rainfall during late summer (Butler et al. 2008). Molt requires substantial food resources (Murphy and King 1992, Bonier et al. 2007), which may not be available to insectivores such as the vireo if conditions in late summer are dry in response to a sharp decline in rainfall (Rohwer et al. 2005, Butler et al. 2008). For this reason, other species that co-occur with the vireo on their Texas breeding range, such as painted bunting (*Passerina ciris*; Thompson 1991) and ash-throated flycatcher (*Myiarchus cinerascens*; Butler et al. 2006) move to the Mexican monsoon region prior to molt. If the black-capped vireo similarly moved into higher-altitude winter sites that received rainfall from the monsoons before molting, this would likely explain more negative δ^2H values.

The choice of feathers to collect for this study was dependent on an understanding of their molt schedules and is thus dependent on the assumption that the feathers collected are molted on the breeding grounds. This assumption was based on information provided in Pyle (1997), which was the best available information at the time, although more recent research by Butler et al. (2008) demonstrated that the species does molt all of the feathers of interest to this study on the breeding grounds. Therefore,

the depleted δ^2H values exhibited by samples in this study are unlikely to result from vireos moving to the higher-altitude monsoon region of Mexico prior to molt.

However, a different version of the high-altitude molt explanation is that most of the δ^2H-depleted samples collected on the wintering grounds originated at higher altitude breeding sites in northern Mexico. In Coahuila, for example, elevations from which vireos have been found, such as those used in this study, exceed 1,500m. Additionally, limited surveys in Coahuila indicate that population densities may be relatively high (Benson and Benson 1990, 1991, McKinney 1998, Farquhar and Gonzalez 2005). Researchers have recently discovered black-capped vireos breeding at least 700km further south into Nuevo León and southwestern Tamaulipas states than any previous confirmed breeding records (Farquhar and Gonzalez 2005, Contreras-Balderas et al. 2012). The southward expansion of known range limits and the relatively large densities of vireos in Coahuila suggest the possibility at least that a higher proportion of the total vireo population comes from high-altitude Mexican breeding sites than from Texas or Oklahoma. If so, then samples with depleted δ^2H values that were collected on the wintering grounds may be from vireos that breed (and molt their feathers) at high-altitude Mexican locations.

However, this possibility still would not explain the depleted feather samples that were collected at lower-altitude breeding sites in Oklahoma and particularly central Texas. The most depleted samples for any collection state on either the breeding or the wintering grounds were those collected at Fort Hood (mean δ^2H= -66.2‰), and by a considerable margin (e.g., the next most depleted samples were from Oklahoma, mean

δ^2H= -54.1‰). Yet, it remains possible that one of the other factors previously discussed is influencing the isotope values in Texas, and possibly Oklahoma too, and the high-altitude molting explanation from northern Mexico explains the majority of depleted samples collected across the wintering range. Indeed, the mean δ^2H value for all feathers collected across the wintering range (-44.6‰) closely approximates that of Coahuila (-45.2‰).

I have described several potential explanations for the unusually depleted δ^2H values in some of my feather tissues, some of which are more probable scenarios than others. However, it is important to keep in mind that all of these explanations are mostly just speculation at this point. Due to the small size of black-capped vireo feathers, all feather material was used in the isotopic analyses, so we cannot run additional analyses without collecting additional feathers. I would suggest that collecting and analyzing additional vireo feather samples from sites across the breeding range would be a useful first step in trying to understand the results from this study. Likewise, collection and analysis of feathers from other resident birds at sites such as Fort Hood would be useful in determining if the patterns observed here are consistent across species from the same sites. Similarly, it would be useful to test groundwater samples from sites across the range, or at least on or near Fort Hood, to determine how groundwater may be influencing the patterns observed here. Depending on the results of an analysis of isotopes in the local groundwater, it may be valuable to study in more detail the underlying hydrology of the aquifers at sites such as Fort Hood.

CHAPTER V

CONCLUSIONS

The research presented in this dissertation came about in response to the need for more information about the winter ecology of the endangered black-capped vireo. Both the Black-capped Vireo Recovery Plan (U.S. Fish and Wildlife Service 1991) and the Black-capped Vireo Population and Habitat Viability Assessment Report (U.S. Fish and Wildlife Service 1996) identified the study of this species during the nonbreeding period as a top research priority. Despite the fact that the black-capped vireo spends less than half of its annual life cycle on the breeding grounds, almost all research, management, and publications concerning this species have focused on the breeding grounds. Very little information exists on essentially every aspect of their winter ecology, including distribution, habitat use, foraging ecology, diet, behavior, interspecific associations with other birds, space use, site fidelity, territoriality, density, and survivorship.

Considering logistical limitations and the breadth of topics to be addressed, I selected three areas of research that I thought could best improve our scientific understanding of the winter ecology of the black-capped vireo. First, I wanted to learn more about winter distribution considering the ecological and conservation importance of understanding distributions for any species. Almost all location records prior to this research were anecdotal in nature, other than some surveys limited in scope only to Sinaloa and/or Nayarit (e.g., Graber 1961, Marshall et al. 1985, Gonzalez-Medina et al. 2009). Investigations across 8 states documented winter occupancy in the 5 most

northern states surveyed (Sinaloa, Durango, Nayarit, Jalisco, and Colima) and did not locate any vireos in the 3 most southern states (Michoacán, Guerrero, and Oaxaca). It is possible, however, that the inability to locate vireos in the southern states was influenced by a combination of logistic and time constraints, reduced manpower, and surveying after spring migration had commenced. My studies of the distribution of the vireo across its winter range also revealed evidence of differential migration, specifically a strong association between age/sex class and winter latitude whereby adult males occupied more northern latitudes than did females and juveniles.

The second primary area of my research focused on a quantitative analysis of habitat use by the black-capped vireo on its winter grounds because patterns of habitat use are as important as distributional patterns from an ecological and conservation point of view. This investigation indicated that black-capped vireos appear to be more habitat generalists during the winter period than they are during the breeding period. I also found that increasing values of slope and foliage cover, and decreasing values of canopy cover and tree diameter, best predicted winter habitat occupancy by black-capped vireos.

The final component of my research attempted to use stable isotopes in black-capped vireo feathers to gain a better understanding of the migration ecology of the species. If feathers collected on the wintering grounds could be used to assess breeding origins of black-capped vireos, then I could examine if any relationship exists between breeding and wintering latitudes such as chain or leapfrog migration. Feathers collected across both the breeding and wintering grounds exhibited high variability in isotope values and thus did not provide sufficient information to establish migratory linkages

between breeding and wintering sites. To better understand why so many samples, particularly those collected in Texas, showed unexpectedly depleted isotope values, more research is needed such as analyzing additional feathers across the breeding range and testing groundwater as a potential source of influence. Additionally, the ability to link wintering sites with breeding sites may be limited by the altitudinal variation in black-capped vireo occupancy of breeding sites in mountainous northern Mexico. Altitude has a known influence on isotope data, and thus if vireos occupy a wide variety of altitudes at breeding sites, then the expected isotope values will also exhibit wide variety. In this study, the expected values for δ^2H in Coahuila almost entirely encompassed the expected values for Oklahoma and Texas, making it difficult to discriminate the breeding origins of feathers collected on the wintering grounds.

This study is the first comprehensive investigation of both the distribution and habitat use of black-capped during the winter period. It also is the first evidence of latitudinal sexual segregation among black-capped vireo across the wintering grounds. A longer migration distance for females relative to males may result in higher mortality rates for females (e.g., Stouffer and Dwyer 2003, Catry et al. 2005, Donald 2007) and explain male-biased adult sex ratios for the black-capped vireo (Graber 1961, Tazik 1991, Grzybowski 1995), which ultimately may have led to the evolution of sexual dichromatism in the species (Marra and Holmes 2001). Differential migration also may explain the earlier arrival of male black-capped vireos relative to conspecific females at the breeding grounds (i.e. protandry; Coppack and Pulido 2009), which has many other potential implications for the ecology and conservation of the species.

Some of the ideas generated from this research suggest several avenues for future inquiry. The implications of carryover effects, how patterns of habitat quality, food availability, and body condition affect the timing of migration and success (e.g., reproductive success, survival) during subsequent periods of an individual's annual cycle, are important to understanding the ecology and conservation of any species. I suggest that future research of black-capped vireos evaluates the importance of carryover effects.

On the breeding grounds, more information is needed concerning molt patterns, adult sex ratios, sex-biased differences in return rates from the winter grounds, and the relationship between the degree of protandry within a population and the intensity of competition for mates, such as in the form of sexual dichromatism, sexual size dimorphism, or extra-pair paternity. Additionally, investigations of sexual selection can examine if there is a relationship between the intensity of dichromatism and mortality rates among individuals such that males with brighter plumage characteristics have relatively higher mortality rates. On the winter grounds, there is much still to learn, and I identified many topics for research earlier in this chapter. Additionally, insights into the timing of spring migration (i.e., do males depart the winter grounds before females) would provide valuable insight about their migration system, and tracking vireos with geolocators should be considered as a means to learn about migratory connectivity while avoiding some of the pitfalls I encountered in the isotope study (e.g., Hallworth et al. 2013, McKinnon et al. 2013). I would recommend that other future research focus on more intensive study of individual populations at a set winter study site (such as at a

field station, which was not available for this study), such that individual birds could be tracked and studied across the entire winter period. This would be more conducive to research topics such as foraging ecology, diet, behavior, interspecific associations with other birds, space use, territoriality, density, survivorship, and fall departure schedules.

The results from my analysis of habitat use indicated that thorn forest habitat may be most suitable for vireo occupancy during the winter months, which is a concern because the thorn forests of western Mexico are most susceptible to clearing for conversion to agriculture (e.g., Dirzo 1994, Rohwer et al. 2009, Rohwer 2013). More broadly, deforestation is the major threat for the long-term conservation of all of the tropical dry forests of western Mexico (Lugo 1988, Masera et al. 1997, Rickers et al. 2007, Galicia et al. 2008). It is unlikely that protected areas will be sufficient to protect winter vireo habitat in Mexico as protected areas in Mexico containing tropical dry forest are scarce (Trejo and Dirzo 2000, Mas and Perez-Vega 2005) and differ widely in their legal status and their actual functioning in practice (Cue-Bar et al. 2006).

One additional conservation concern for the black-capped vireo and many other migratory songbirds that spend the winter in Mexico is climate change. Over the last half century across southern Mexico, there have been linear increases of both mean monthly temperatures and maximum temperatures (Englehart and Douglas 2005, Peralta-Hernandez et al. 2008), and climate models project a continued pattern of increasing temperatures and decreasing precipitation across western Mexico (IPCC 2001, Gomez-Mendoza and Arriaga 2007, Saenz-Romero et al. 2010). One projected pattern resulting from this is a change in the distribution of vegetative associations,

which has implications for conservation efforts such as natural protected areas. Villers-Ruiz and Trejo-Vasquez (1998) concluded that of 33 natural protected forest areas in Mexico, only 9 would remain in the same life zones under global climate change. The extent of tropical dry forests may expand under these expected changes (Leemans (1989), although evaporative demands by the vegetation may also increase, reducing water runoff rates and overall water availability for productive activities, which may lead to an increase of secondary forests (Vose and Maass 1999). It seems likely that black-capped vireos would occupy these secondary forests under this scenario, although the relative value of these forests as winter habitat to vireos is unknown.

Lastly, tracking the relationships of black-capped vireo habitat use on the wintering grounds and climate change will be critical to the conservation of this species. One concern under a future climate change scenario relates to the timing of the black-capped vireos migration patterns. Although many species have advanced the timing of their spring arrival and breeding seasons to coincide with warming temperatures on the breeding grounds (e.g., Dunn and Winkler 1999, Cotton 2003, Murphy-Klassen et al. 2005), such adaptive responses may be constrained for other species in the future by conditions during the nonbreeding season. If departure dates by migratory birds depend upon pre-migratory fueling on arthropods (Brown and Sherry 2006b), which itself depends upon rainfall, then projections of decreasing precipitation patterns across western Mexico suggests there will be delays in the timing of spring migration for migratory songbirds such as the black-capped vireo at the very time when the adaptive response to changing conditions on the breeding grounds would be selection for earlier

spring departure dates (e.g., Studds and Marra 2007). Furthermore, intensity of rainfall events has increased across western Mexico (Garcia-Paez and Cruz-Medina 2009, Peralta-Hernandez et al. 2009); the pattern of decreased total rainfall occurring in more intense events suggests that rainfall patterns will become increasingly variable, as will arthropod availability for migratory birds as a result. Such variation in non-breeding season rainfall may be particularly concerning for species with small populations or restricted winter distributions (Studds and Marra 2007), such as the black-capped vireo, and may differentially affect males and females considering the latitudinal sexual segregation described in this study.

REFERENCES

Agresti, A. 2007. An introduction to categorical data analysis. Second edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Alisauskas, R. T., and K. A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49–54.

Alves, J. A., T. G. Gunnarsson, D. B. Hayhow, G. F. Appleton, P. M. Potts, W. J. Sutherland, and J. A. Gill. 2013. Costs, benefits, and fitness consequences of different migratory strategies. Ecology 94:11–17.

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

Amrhein, V., H. Kunc, R. Schmidt, and M. Naguib. 2007. Temporal patterns of territory settlement and detectability in mated and unmated nightingales *Luscinia megarhynchos*. Ibis 149:237–244.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.

Apan, A. A., and J. A. Peterson. 1998. Probing tropical deforestation: the use of GIS and statistical analysis of georeferenced data. Applied Geography 18:137–152.

Arbingast, S. A., C. P. Blair, J. R. Buchanan, C. C. Gill, R. K. Holz, C. A. Marin-R, R. H. Ryan, M. E. Bonine, J. P. Weiler. 1975. Atlas of Mexico. Second edition. Bureau of Business Research, University of Texas, Austin, USA.

Armesto, J. J., and J. A. Martinez. 1978. Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. Journal of Ecology 66:881–889.

Askins, R. 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, New Haven, Connecticut, USA.

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7:1–57.

Athrey, G., R. F. Lance, and P. L. Leberg. 2012. How far is too close? restricted, sex-biased dispersal in black-capped vireos. Molecular Ecology 21:4359–4370.

Badyaev, A. V., and G. E. Hill. 2000. Evolution of sexual dichromatism: contribution of carotenoid-versus melanin-based coloration. Biological Journal of the Linnaean Society 69:153–172.

Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology Evolution and Systematics 34:27–49.

Baker, R. R., and G. A. Parker. 1979. The evolution of bird coloration. Philosophical Transactions of the Royal Society of London Series B 287:63–130.

Balda, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in south-eastern Arizona. Condor 71:399–412.

Barber, D. R. 1993. Effects of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Thesis, University of Arkansas, Fayetteville, USA.

Barbier, E. B., and J. C. Burgess. 1996. Economic analysis of deforestation in Mexico. Environment and Development Economics 1:203–239.

Barlow, J. C. 1980. Patterns of ecological interaction among migrant and resident vireos on the wintering grounds. Pages 79–108 *in* A. Keast, and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C., USA.

Barr, K. R., D. L. Lindsay, G. Athrey, R. F. Lance, T. J. Hayden, S. A. Tweddale, and P. L. Leberg. 2008. Population structure in an endangered songbird: maintenance of genetic differentiation despite high vagility and significant population recovery. Molecular Ecology 17:3628–3639.

Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London Series B 271, Biology Letters Supplement 4:S215–S218.

Beaty, R. M., and A. H. Taylor. 2001. Spatial and temporal variation of fire regimes in a mixed conifer landscape, Southern Cascades, California, USA. Journal of Biogeography 28:955–966.

Bell, C. P. 2005. Inter- and intrapopulation migration patterns. Pages 41–52 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Bell, H. L. 1985. Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. Australian Journal of Ecology 10:207–221.

Benkman, C. W. 1997. Feeding behavior, flock-size dynamics, and variation in sexual selection in crossbills. Auk 114:163–178.

Bennett, A. T. D., I. C. Cuthill, and K. J. Norris. 1994. Sexual selection and the mismeasure of color. American Naturalist 144:848–860.

Benson, R. H., and K. L. P. Benson. 1990. Estimated size of black-capped vireo population in northern Coahuila, Mexico. Condor 92:777–779.

Benson, R. H., and K. L. P. Benson. 1991. Reply to Scott and Garton. Condor 93:470–472.

Berthold, P. 2001. Bird migration. Oxford University Press, Oxford, United Kingdom.

Bessa-Gomes, C., S. Legendre, and J. Clobert. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. Ecology Letters 7:802–812.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs No. 43. American Ornithologists' Union. Washington, D. C., USA.

Blake, J. G., and B. A. Loiselle. 1992. Habitat use by Neotropical migrants at La Selva Biological Station and Braulio Carrillo National Park, Costa Rica. Pages 257–272 *in* J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Pages 35–91 *in* D. M. Power, editor. Current Ornithology, Vol. 11. Plenum Press, New York, USA.

Bonier, F., P. R. Martin, J. P. Jensen, L. K. Butler, M. Ramenofsky, and J. C. Wingfield. 2007. Pre-migratory life history stages of juvenile arctic birds: costs, constraints, and trade-offs. Ecology 88:2729–2735.

Bowen, G. J. 2010. Isoscapes: spatial pattern in isotopic biogeochemistry. Annual Review of Earth and Planetary Sciences 38:161–187.

Bowen, G. J., and J. Revenaugh. 2003. Interpolating the isotopic composition of modern meteoric precipitation. Water Resources Research 39, 1299, doi:10.129/2003WR002086.

Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005. Global applications of stable hydrogen and oxygen isotopes to wildlife forensics. Oecologia 143:337–348.

Bowen, G. J., and B. Wilkinson. 2002. Spatial distribution of $\delta^{18}O$ in meteoric precipitation. Geology 30:315–318.

Bowen, S., and P. Gerritsen. 2007. Reverse leasing and power dynamics among blue agave farmers in southern Jalisco, Mexico. Agriculture and Human Values 24:473–488.

Breitwisch, R. 1989. Mortality patterns, sex ratios and parental investment in monogamous birds. Current Ornithology 6:1–50.

Brown, D. R., and T. W. Sherry. 2006a. Behavioral response of Jamaican birds to dry season food supplementation. Biotropica 38:91–99.

Brown, D. R., and T. W. Sherry. 2006b. Food supply controls physical condition of a long distance migrant bird wintering in the tropics. Oecologia 149:22–32.

Bruggemann, N., A. Kessler, Z. Kayler, S. G. Keel, F. Badeck, F., M. Barthel, P. Boeckx, N. Buchmann, E. Brugnoli, J. Esperschütz, O. Gavrichkova, J. Ghashghaie, N. Gomez-Casanovas, C. Keitel, A. Knohl, D. Kuptz, S. Palacio, Y. Salmon, Y Uchida, and M. Bahn. 2011. Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review. Biogeosciences 8:3457–3489.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53:603–618.

Burgos, A., and J. M. Maass. 2004. Vegetation change associated with land-use in tropical dry forest areas of western Mexico. Agriculture, Ecosystems and Environment 104:475–481.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, USA.

Butler, L. K., T. J. Hayden, and L. M. Romero. 2008. Prebasic molt of black-capped and white-eyed vireos: effects of breeding site and the El Nino-Southern Oscillation. Condor 110:428–440.

Butler, L. K., S. Rowher, and M. Rogers. 2006. Prebasic molt and molt-related movements in ash-throated flycatchers. Condor 108:647–660.

Calder, W. A. 1974. Consequences of body size for avian energetics. Pages 84–144 *in* R. A. Paynter, Jr., editor. Avian energetics. Nuttall Ornithological Club Publication 15.

Campbell, L. 1995. Endangered and threatened animals of Texas: their life history and management. Texas Parks and Wildlife Press, Austin, USA.

Castillo, A., A. Magana, A. Pujadas, L. Martinez, and C. Godinez. 2005. Understanding the interaction of rural people with ecosystems: a case study in a tropical dry forest of Mexico. Ecosystems 8:630–643.

Catry, P., M. Lecoq, A. Araujo, G. Conway, M. Felgueiras, J. M. B. King, S. Rumsey, H. Salima, and P. Tenreiro. 2005. Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. Journal of Avian Biology 36:184–190.

Ceballos, G., and A. Garcia. 1995. Conserving Neotropical biodiversity: the role of dry forests in western Mexico. Conservation Biology 9:1349–1353.

Ceballos, G., and D. Navarro. 1991. Diversity and conservation of Mexican mammals. Pages 167–198 *in* M. A. Mares and D. J. Schmidly, editors. Latin American mammalogy: history, biodiversity, and conservation. University of Oklahoma Press, Norman, USA.

Challenger, A. 1998. Utilizacion y conservacion de los ecosistemas terrestres de Mexico. Pasado, presente y futuro. Comision Nacional para el Conocimiento y Uso de la Biodiversidad and Instituto de Biologia Universidad Nacional Autonóma de México, Mexico, Distrito Federal, Mexico. [In Spanish.]

Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109:132–141.

Chandler, C. R., and R. S. Mulvihill. 1990. Wing-shape variation and differential timing of migration in dark-eyed juncos. Condor 92:54–61.

Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. Bioscience 31:107–113.

Colorado Plateau Stable Isotope Laboratory [CPSIL]. 2013. What are stable isotopes? <http://www.isotope.nau.edu/isotope.html>. Accessed 4 September 2013.

Comicion Nacional para el Conocimiento y Uso de la Biodiversidad [CONABIO]. 1999. Uso de suelo y vegetacion modificado por CONABIO. Escala 1: 1,000,000. CONABIO. Distrito Federal, Mexico. [In Spanish.]

Contreras-Balderas, A. J., O. Ballesteros-Medrano, and J. A. García-Salas. 2012. Black-capped vireo (*Vireo atricapilla*) in urban areas of Monterrey, Nuevo León, Mexico. Southwestern Naturalist 57:212–213.

Cooper, S. M., and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. Oecologia 68:446–455.

Coplen, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Communications in Mass Spectrometry 25:2538–2560.

Coppack, T., and F. Pulido. 2009. Proximate control and adaptive potential of protandrous migration in birds. Integrative and Comparative Biology 49:493–506.

Coppack, T., A. P. Tottrup, and C. Spottiswoode. 2006. Degree of protandry reflects level of extrapair paternity in migratory songbirds. Journal of Ornithology 147:260–265.

Corcuera, P., and J. E. L. Butterfield. 1999. Bird communities of dry forests and oak woodland of western Mexico. Ibis 141:240–255.

Corcuera, P., and J. A. Zavala-Hurtado. 2006. The influence of vegetation on bird distribution in dry forests and oak woodlands of western Mexico. International Journal of Tropical Biology and Conservation 54:657–672.

Cox, G. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist 126:451–474.

Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: latitudinal segregation by age and sex class. Pages 33–38 *in* V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, editors. Current Ornithology, Vol. 15. Plenum Press, New York, USA.

Cue-Bar, E. M., J. L. Villasenor, J. J. Morrone, and G. Ibarra-Manriquez. 2006. Identifying priority areas for conservation in Mexican tropical deciduous forest based on tree species. Interciencia 31:712–719.

Cuthill, I.C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. American Naturalist 153:183–200.

Davis, J. 1960. Notes on the birds of Colima, Mexico. Condor 62:215–219.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. C. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproduction to future survival. Proceedings of the Royal Society of London Series B 267:2093–2098.

Deininger, K. W., and B. Minten. 1999. Poverty, policies, and deforestation: the case of Mexico. Economic Development and Cultural Change 47:313–344.

De la Hera, I., J. Perez-Tris, and J. L. Telleria. 2010. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. Journal of Avian Biology 41:609–614.

Dirzo, R. 1994. Mexican diversity of flora. P. R. Gil, editor. Natural and cultural diversity of Mexico. Cemex and Agrupacion Sierra Madre, Distrito Federal, Mexico.

Doherty, P. F., Jr., G. Sorci, J. A. Royle, J. E. Hines, J. D. Nichols, and T. Boulinier. 2003. Sexual selection affects local extinction and turnover in bird communities. Proceedings of the National Academy of Sciences 100:5858–5862.

Donald, P. F. 2007. Adult sex ratios in wild bird populations. Ibis 149:671–692.

Douglas, M. W., R. A. Maddox, K. Howard, and S. Reyes. 1993. The Mexican monsoon. Journal of Climate 6:1665–1677.

Dueser, R. D., and H. H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89–98.

Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile sage grouse. Journal of Wildlife Management 50:228–235.

Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. Evolution 55:161–175.

Eaton, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monomorphic" birds. Proceedings of the National Academy of Sciences 102:10942–10946.

Eaton, M. D. 2007. Avian visual perspective on plumage coloration confirms rarity of sexually monochromatic North American passerines. Auk 124:155–161.

Eliason, S. A., and E. B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. Restoration Ecology 5:245–255.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34:76–91.

Endler, J. A. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. Environmental Biology of Fishes 9:173–190.

Englehart, P. J., and A. V. Douglas. 2005. Changing behavior in the diurnal range of surface air temperatures over Mexico. Geophysical Research Letters 32:, L01701, DOI: 10.1029/2004GL021139.

Escalante, P., A. G. Navarro, and A. T. Peterson. 1993. A geographical, ecological, and historical analysis of land bird diversity in Mexico. Pages 281–307 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, USA.

Escalona, G., M. Torres, A. G. Navarro, R. Villalon, B. Hernandez, and H. Benitez. 1995. Migratory birds of the cloud forests of Mexico. Pages 15–33 *in* M. H. Wilson and S. A. Sader, editors. Conservation of Neotropical migratory birds in Mexico. Maine Agricultural and Forest Experiment Station Misc. Pub. 727.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson III, and N. Warnock. 2010. Conserving migratory land birds in the New World: do we know enough? Ecological Applications 20:398–418.

Farquhar, C. C., and J. I. Gonzalez. 2005. Breeding habitat, distribution and population status of the black-capped vireo in northern Mexico. Project WER65 Final Report. U. S. Fish and Wildlife Service, Austin, Texas, USA.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, United Kingdom.

Foose, T. J., L. de Boer, U. S. Seal, and R. Lande. 1995. Conservation management strategies based on viable populations. Pages 274–294 *in* J. D. Ballou, M. Gilpin, and T. J. Foose, editors. Population management for survival and recovery. Columbia University Press, New York, USA.

Francis, C. M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548–556.

Franklin, J., P. McCullough, and C. Gray. 2000. Terrain variables used for predictive mapping of vegetation communities in southern California. Pages 331–354 *in* J. P. Wilson and J. C. Gallant, editors. Terrain analysis: principles and applications. Wiley, New York, USA.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monographs in Population Biology 5. Princeton University Press, Princeton, New Jersey, USA.

Friedman, I., J. M. Harris, G. I. Smith, and C. A. Johnson. 2002. Stable isotope composition of waters in the Great Basin, United States. 1. Air mass trajectories. Journal of Geophysical Research 107, D19. doi:10.1029/2001JD000566.

Friedman, N. R., C. M. Hofmann, B. Kondo, and K. E. Omland. 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). Evolution 63:3269–3274.

Froehlich, D. R., S. Rohwer, and B. J. Stutchbury. 2005. Spring molt constraints versus winter territoriality. Pages 321–335 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds; the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Galicia, L., A. E. Zarco-Arista, K. I. Mendoza-Robles, J. L. Palacio-Prieto, and A. Garcia-Romero. 2008. Land use/cover, landforms and fragmentation patterns in a tropical dry forest in the southern Pacific region of Mexico. Singapore Journal of Tropical Geography 29:137–154.

Gallardo-Cruz, J., E. A. Perez-Garcia, and J. A. Meave. 2009. *B*-diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. Landscape Ecology 24:473–482.

Garcia-Paez, F., and I. R. Cruz-Medina. 2009. Variability of rainfall in the North Pacific Region of Mexico. Agrociencia 43:1–9.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, USA.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. Pages 17–54 *in* P. P. G. Bateson, and P. H. Klopfer, editors. Perspectives in ethology, Vol. 3. Plenum, New York, USA.

Gauthreaux, S. A., Jr. 1982. The ecology and evolution of avian migration systems. Pages 93–168 *in* D. S. Farmer, J. R. King, and K. C. Parkes, editors. Avian biology. Volume 6. Academic Press, New York, USA.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75:1–34.

Gentry, A. H. 1995. Diversity and floristic composition of Neotropical dry forests. Pages 146–194 *in* S. H. Bullock, H. A. Mooney, and E. Medina, editors. Seasonally dry tropical forests. Cambridge University Press, Cambridge, United Kingdom.

Gerritsen, P. 1998. Community development, natural resource management and biodiversity conservation in the Sierra de Manantlan Biosphere, Mexico. Community Development Journal 33:314–324.

Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436–438.

Githiru, M., L. Lens, L. A. Bennun, and C. Perrins. 2006. Experimental evidence of 'floaters' in two isolated populations of an Afrotropical forest bird. Ostrich 77:28–35.

Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. Journal of Animal Ecology 87:193–210.

Gloutney, M. L., and K. A. Hobson. 1998. Field preservation techniques for the analysis of stable-carbon and nitrogen isotope ratios in eggs. Journal of Field Ornithology 69:223–227.

Gomez-Mendoza, L., and L. Arriaga. 2007. Modeling the effect of climate change on the distribution of oak and pine species of Mexico. Conservation Biology 21:1545–1555.

Gonzalez-Medina, E., U. T. Angulo-Gastelum, J. A. Castillo-Guerrero, and M. Guevara-Medina. 2009. Distribución y abundancia relative invernal del vireo de cabeza negra (*Vireo atricapilla*) en Sinaloa, Mexico. Ornitología Neotropical 20:291–298.

Gordon, J. E., W. D. Hawthorne, A. Reyes-Garcia, G. Sandoval, and A. J. Barrance. 2004. Assessing landscapes: a case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and southern Honduras. Biological Conservation 117:429–442.

Gove, A. D., J. D. Majer, and V. Rico-Gray. 2005. Methods for conservation outside of formal reserve systems: the case of ants in the seasonally dry tropics of Veracruz, Mexico. Biological Conservation 126:328–338.

Graber, J. 1957. A bioecological study of the black-capped vireo (*Vireo atricapilla*). Dissertation, University of Oklahoma, Norman, USA.

Graber, J. 1961. Distribution, habitat requirements, and life history of the black-capped vireo (*Vireo atricapilla*). Ecological Monographs 31:313–336.

Graves, G. R., C. S. Romanek, and A. R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proceedings of the National Academy of Sciences 99:8096–8100.

Greenberg, R. 1986. Competition in migrant birds in the non-breeding season. Current Ornithology 3:281–307.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. Pages 273–286 *in* J. M. Hagan, III, and D. W. Johnston, editors. Conservation of

Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Greenberg, R. 1995. Insectivorous migratory birds in tropical ecosystems: the breeding currency hypothesis. Journal of Avian Biology 26:260–264.

Greenberg, R., and P. Bichier. 2005. Determinants of tree species preference of birds in oak-acacia woodlands of Central America. Journal of Tropical Ecology 21:57–66.

Greenberg, R., P. Bichier, and J. Sterling. 1997. Acacia, cattle, and migratory birds in southeastern Mexico. Biological Conservation 80:235–247.

Groombridge, B., and M. D. Jenkins. 2000. Global biodiversity: Earth's living resources in the 21st Century. United Nations Environment Programme. World Conservation Press, Cambridge, United Kingdom.

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapillus*). Account 181 *in* A. Poole and F. Gill, editors. The birds of North America, The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C., USA.

Grzybowski, J. A., D. J. Tazik, and G. D. Schnell. 1994. Regional analysis of black-capped vireo breeding habitats. Condor 96:512–544.

Gunnarsson, T. G., J. A. Gill, P. W. Atkinson, G. Gelinaud, P. M. Potts, R. E. Croger, G. A. Gudmundsson, G. F. Appleton, and W. J. Sutherland. 2006. Population-scale drivers of individual arrival times in migratory birds. Journal of Animal Ecology 75:1119–1127.

Guthery, F. S., and R. L. Bingham. 2007. A primer on interpreting regression models. Journal of Wildlife Management 71:684–692.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra. 2013. Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? Auk 130:273–282.

Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Haskell, D. G. 1996. Do the bright plumages of birds incur a cost due to nest predation? Evolutionary Ecology 10: 285–288.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology 79:2376–2390.

Helmer, E. H. 2000. The landscape ecology of tropical secondary forest in montane Costa Rica. Ecosystems 3:98–114.

Hespenheide, H. A. 1980. Bird community structure in two Panama forests: residents, migrants, and seasonality during the non-breeding season. Pages 227–238 *in* A. E. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C., USA.

Heywood, J. S. 1989. Sexual selection by the handicap mechanism. Evolution 43:1387–1397.

Hilden, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. 1999. Oecologia 120:314–326.

Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. Diversity and Distributions 11:157–164.

Hobson, K. A., R. Barnett-Johnson, and T. Cerling. 2010. Using isoscapes to track animal migration. Pages 273–298 *in* J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu. Isoscapes. Springer, The Netherlands.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diets using stable isotopes. II. Factors influencing diet-tissue fractionation. Condor 94:181–188.

Hobson, K. A., H. L. Gibbs, and M. L. Gloutney. 1997. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. Canadian Journal of Zoology 75:1720–1723.

Hobson, K. A., K. P. McFarland, L. I. Wassenaar, C. C. Rimmer, and J. E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's thrushes using stable isotope analyses of feathers. Auk 118:16–23.

Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, R. L. Powell, C. J. Still, and J. M. Craine. 2012. A multi-isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) feather isoscape to assign Afrotropical migrant birds to origins. Ecosphere 3: art44. <http://dx.doi.org/10.1890/ES12-00018.1>. Accessed 5 September 2013.

Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotope ratios of animal tissues. Proceedings of the National Academy of Sciences 96:8003–8006.

Hobson, K. A., and L. I. Wassenaar. 1999. Stable isotope analysis: an introduction. Oecologia 120:312–313.

Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9–18.

Hoefs, J. 2009. Stable isotope geochemistry. Sixth edition. Springer-Verlag, Berlin, Germany.

Hoelzer, G. A. 1989. The good parent process of sexual selection. Animal Behaviour 38:1067–1078.

Holberton, R. L. 1993. An endogenous basis for differential migration in the dark-eyed junco. Condor 95:580–587.

Holland, B., and W. R. Rice. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. Proceedings of the National Academy of Sciences 96:5083–5088.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35.

Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology 66:720–728.

Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. Pages 563–575 *in* J. M. Hagan, III, and D. W. Johnston, editors. Conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA

Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality, and overwinter survival of two migrant warbler species in Jamaica. Condor 91:545–561.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56:201–220.

Houston, D. R. 2008. Foraging behavior of the black-capped vireo in central Texas. Thesis, Texas State University, San Marcos, USA.

Howell, S. N. G. 1999. A bird-finding guide to Mexico. Cornell University Press, Ithaca, New York, USA.

Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and northern central America. Oxford University Press, New York, USA.

Howell, T.R. 1953. Racial and sexual differences in migration in *Sphyrapicus varius*. Auk 70:118–126.

Huggett, R. J. 1998. Fundamentals of biogeography. Routledge, New York, USA.

Hutto, R. L. 1985. Habitat selection by non-breeding, migratory landbirds. Pages 455–476 *in* M. Cody, editor. Habitat selection in birds. Academic Press, New York, USA.

Hutto, R. L. 1988. Is tropical deforestation responsible for the reported declines in Neotropical migrant populations? American Birds 42:375–379.

Hutto, R. L. 1992. Habitat distributions of migratory landbird species in western Mexico. Pages 211–239 *in* J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. Condor 96:105–118.

Instituto Manantlán de Ecología y Conservación de la Biodiversidad [IMECBIO]. 1998. Diagnostico integral y plan comunitario de los recursos naturales: Ejido Zenzontla, Municipio de Tuxcacuesco, Jalisco. IMECBIO, Universidad de Guadalajara, Autlan, Jalisco, Mexico. [In Spanish.]

Intergovernmental Panel on Climate Change [IPCC]. 2001. Climate change 2001: synthesis report. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Janzen, D. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.

Janzen, D. 1988. Tropical dry forest, the most endangered major tropical ecosystem. Pages 130–137 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D. C., USA.

Janzen, D., and T. W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49:96–110.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, D. H. 1981. The use and misuse of statistics in wildlife habitat studies. Pages 11–19 *in* D. E. Capen, editor. The use of multivariate statistics in studies of wildlife habitat. U. S. Forest Service Gen. Tech. Report RM-87. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology 20:1433–1444.

Johnston, D. W. 1970. Age and sex distribution in indigo buntings. Bird Banding 41:113–118.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:556–562.

Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. Ecology 64:1481–1494.

Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

Kendeigh, S. C. 1945. Resistance to hunger in birds. Journal of Wildlife Management 9:217–226.

Ketterson, E. D., and V. Nolan, Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). Ecology 57:679–693.

Ketterson, E. D., and V. Nolan, Jr. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of dark-eyed juncos (*Junco hyemalis*). Auk 96:532–536.

Ketterson, E. D., and V. Nolan, Jr. 1983. The evolution of differential bird migration. Pages 357–402 *in* R. F. Johnston, editor. Current Ornithology, Vol. 1. Plenum Press, New York, USA.

King, J. R., D. S. Farner, and L. R. Mewaldt. 1965. Seasonal sex and age ratios in populations of the white-crowned sparrows of the race *gambelii*. Condor 67:489–504.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1–12.

Kissner, K. J., P. J. Weatherhead, and C. M. Francis. 2003. Sexual size dimorphism and timing of spring migration in birds. Journal of Evolutionary Biology 16:154–162.

Koch, P. L., J. Heisinger, C. Moss, R. W. Carlson, M. L. Fogel, and A. K. Behrensmeyer. 1995. Isotopic tracking of change in diet and habitat use in African elephants. Science 267:1340–1343.

Koehler, B., M. D. Corre, K. Steger, R. Well, E. Zehe, J. P. Sueta, and E. Veldkamp. 2012. An in-depth look into a tropical lowland forest soil: nitrogen-addition effects on the content of N_2O, CO_2, and CH_4 and N_2O isotopic signatures down to 2-m depth. Biogeochemistry 111:695–713.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Kokko, H., T. G. Gunnarsson, L. J. Morrell, and J. A. Gill. 2006. Why do female migratory birds arrive later than males? Journal of Animal Ecology 75:1293–1303.

Komar, O., B. J. O'Shea, A. T. Peterson, and A. G. Navarro-Siguenza. 2005. Evidence of latitudinal sexual segregation among migratory birds wintering in Mexico. Auk 122:938–948.

Korner, C., G. D. Farquhar, and S. C. Wong. 1991. Carbon isotope discrimination follows latitudinal and altitudinal trends. Oecologia 88:30–40.

Kostecke, R. M., and D. A. Cimprich. 2008. Adult and juvenile survival of black-capped vireos within a large breeding population in Texas. Condor 110:251–259.

Krementz, D. G., and G. W. Pendleton. 1990. Fat scoring: sources of variability. Condor 92:500–507.

Kricher, J. C., and W. E. Davis, Jr. 1992. Patterns of avian species richness in disturbed and undisturbed habitats in Belize. Pages 240–246 *in* J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Kurz-Besson, C., D. Otieno, R. Lobo do Vale, R. Siegwolf, M. Schmidt, A. Herd, C. Nogueira, T. Soares David, J. Soares David, T. Tenhunen, J. Santos Pereira, and M. Chaves. 2006. Hydraulic lift in cork trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance. Plant and Soil 282:361–378.

Kvarnemo, C., and I. Ahnesjo. 1996. The dynamics of operational sex ratios and competition for mates. Trends in Ecology and Evolution 11:404–408.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, United Kingdom.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:294–305.

Latta, S. C., and J. Faaborg. 2001. Winter site fidelity of prairie warblers in the Dominican Republic. Condor 103:455–468.

Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May warblers wintering in multiple habitats. Ecology 83:2502–2515.

Leal-Sandoval, A., J. Fonseca-Parra, and J. A. Castillo-Guerrero. 2009. Noteworthy bird records from central Sinaloa, Mexico. Huitzil 10:63–65.

Leemans, R. 1989. Possible changes in natural vegetation patterns due to a global warming. Pages 105–122 *in* A. Hackl, editor. *Der Treibhauseffekt: Das Problem - Mögliche Folgen - Erforderliche Maßnahmen*, Akademie für Umwelt and Energie, Laxenburg, Austria.

Lefebvre, G., B. Poulin, and R. McNeil. 1992. Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. Wilson Bulletin 104:400–412.

Lefebvre, G., B. Poulin, and R. McNeil. 2004. Temporal dynamics of mangrove bird communities in Venezuela with special reference to migrant warblers. Auk 111:405–415.

Leisler, B. 1990. Selection and use of habitat of wintering migrants. Pages 156–174 *in* E. Gwinner, editor. Bird migration. Springer-Verlag, Berlin, Germany.

Leopold, A. S. 1959. Wildlife of Mexico: the game birds and mammals. University of California Press, Berkeley, USA.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Lewis, S., S. Benvenuti, L. Dall'Antonia, R. Griffiths, L. Money, T. N. Sherratt, S. Wanless, and K. C. Hamer. 2002. Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of the Royal Society of London Series B 269:1687–1693.

Ligon, J. D. 1999. The evolution of avian breeding systems. Oxford University Press, Oxford, United Kingdom.

Liker, A., and T. Szekely. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. Evolution 59:890–897.

Liu, Z., G. J. Bowen, and J. M. Welker. 2010. Atmospheric circulation is reflected in precipitation isotope gradients reflect atmospheric circulation over the conterminous United States. Journal of Geophysical Research 115, D22120. doi:10.1029/2010JD014175.

Lott, C. A., and J. P. Smith. 2006. A geographic-information-system approach to estimating the origin of migratory raptors in North America using stable hydrogen isotope ratios in feathers. Auk 123:822–835.

Lott, E. J., S. H. Bullock, and J. A. Solis-Magallanes. 1987. Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. Biotropica 19:228–235.

Lower Colorado River Authority [LCRA]. 2007. Balcones Canyonlands Preserve land management plan. Tier III. Lower Colorado River Authority, McGregor Preserve, and Cypress Creek Macrosite.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164–170.

Lugo, A. E. 1988. Estimating reductions in the diversity of tropical forests species. Pages 51–57 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D. C., USA.

Lundberg, P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. Behavior, Ecology, and Sociobiology 17:185–189.

Lynch, J. F. 1989. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. Condor 91:515–544.

Lynch, J. F., E. S. Morton, and M. E. Van der Voort. 1985. Habitat segregation between the sexes on wintering hooded warblers (*Wilsonia citrina*). Auk 102:714–721.

Maass, J. M., P. Balvanera, A. Castillo, G. C. Daily, H. A. Mooney, P. Ehrlich, M. Quesada, A. Miranda, V. J. Jaramillo, F. Garcia-Oliva, A. Martinez-Yrizar, H. Cotler, J. Lopez-Blanco, A. Perez-Jimenez, A. Burquez, C. Tinoco, G. Ceballos, L. Barraza, R. Ayala, and J. Sarukhan. 2005. Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the Pacific Coast of Mexico. Ecology and Society 10:17. <http://www.ecologyandsociety.org/vol10/iss1/art17/ >. Accessed 12 May 2013.

MacGregor-Fors, I., A. G. Navarro-Siguenza, L. Morales-Perez, and J. E. Schondube. 2012. Note on the distribution and migration of the black-capped vireo (*Vireo atricapilla*). Huitzil 13:17–21.

Macias Macias, A. 2001. El cluster en la industria del tequila en Jalisco, Mexico. Agroalimentaria 13:57–72.

Mackenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, Burlington, Massachussetts, USA.

Major, R. E. 1992. Mate guarding in a population of white-fronted chats, *Ephthianura albifrons* Jardine and Selby (Passeriformes, Ephthianuridae) – a response to group living and a male-skewed sex-ratio. Australian Journal of Zoology 40:401–409.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, United Kingdom.

Marcum, C. L., and D. O. Loftsgaarden. 1980. A non-mapping technique for studying habitat preferences. Journal of Wildlife Management 44:963–968.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. Auk 118:92–104.

Marra, P. P., R. T. Holmes, and T. W. Sherry. 1993. Territorial exclusion by a temperate-tropical migrant warbler in Jamaica: a removal experiment with American redstarts (*Setophaga ruticulla*). Auk 110:565–572.

Marshall, J. D., J. R. Brookes, and K. Lajtha. 2007. Sources of variation in the stable isotopic composition of plants. Pages 22–50 *in* R. Michener and K. Lajtha, editors. Stable isotopes in ecology and environmental sciences. Blackwell Publishing, Oxford, United Kingdom.

Marshall, J. T., Jr., R. B. Clapp, and J. A. Grzybowski. 1984. Interim status report: *Vireo atricapillus* Woodhouse, Black-capped vireo. Museum Section, National Museum of Natural History, Washington, D. C., USA.

Marshall, J. T., Jr., R. B. Clapp, and J. A. Grzybowski. 1985. Status report: *Vireo atricapillus* Woodhouse, Black-capped vireo. Office of Endangered Species, U. S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

Martin, T. E., and D. M. Finch. 1995. Ecology and management of Neotropical migrants: a synthesis and review of critical issues. Oxford University Press, New York, USA.

Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. E. Allen, and W. Jenkins. 1997. BBIRD field protocols. Montana Cooperative Wildlife Research Unit, Missoula, Montana, USA.

Martinez-Yrizar, A., A. Burquez, and M. Maass. 2000. Structure and functioning of tropical deciduous forest in western Mexico. Pages 19–35 *in* R. H. Robichaux and D. A. Yetmen, editors. The tropical deciduous forest of Alamos:

biodiversity of a threatened ecosystem in Mexico. University of Arizona Press, Tucson, USA.

Mas, J. F., and A. Perez-Vega. 2005. La representatividad del sistema nacional de areas protegidas (SINAP). INE-SEMARNAT, Mexico. Gaceta Ecologica 74:5–14.

Masera, O. R., M. J. Ordonez, and R. Dirzo. 1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. Climatic Science 35:265–295.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McCleery, R. A., R. R. Lopez, N. J. Silvy, and S. N. Kahlick. 2007. Habitat use of fox squirrels in an urban environment. Journal of Wildlife Management 71:1149–1157.

McClure, C. J. W., B. W. Rolek, and G. E. Hill. 2012. Predicting occupancy of wintering migratory birds: is microhabitat information necessary? Condor 114:482–490.

McFarland, T. M., H. A. Mathewson, J. E. Groce, M. L. Morrison, and R. N. Wilkins. 2013. A range-wide survey of the endangered black-capped vireo in Texas. Southeastern Naturalist 12:41–60.

McFarland, T. M., H. A. Mathewson, M. L. Morrison, R. T. Snelgrove, J. E. Groce, B. A. Collier, and R. N. Wilkins. 2012. Estimating the distribution and abundance of the black-capped vireo in Texas. Texas A&M Institute of Renewable Natural Resources, College Station, USA.

McKellar, A. E., P. P. Marra, and L. M. Ratcliffe. 2013. Starting over: experimental effects of breeding delay on reproductive success in early-arriving American redstarts. Journal of Avian Biology doi: 10.1111/j.1600-048X.2013.00180.x.

McKinney, B. R. 1998. Surveying, monitoring and managing select endangered/threatened species of concern in the Trans-Pecos ecoregion of western Texas. U.S. Fish and Wildlife Service Final Report (No. 1448-20181-97-G932). Texas Parks and Wildlife Department, Austin, USA.

McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. Auk 130:211–222.

McLain, D. K. 1993. Cope's rules, sexual selection, and the loss of ecological plasticity. Oikos 68:490–500.

McLain, D. K., M. P. Moulton, and T. P. Redfearn. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. Oikos 74:27–34.

McLaughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science 167:131–139.

Meehan, T. D., J. T. Giermakowski, and P. M. Cryan. 2004. A GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation

for the use in animal movement studies. Isotopes in Environmental and Health Studies 40:291–300.

Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33:491–505.

Miller, A. H. 1955. The avifauna of the Sierra del Carmen of Coahuila, Mexico. Condor 57:154–178.

Miller, P. M., and J. B. Kauffman. 1998. Effect of slash and burn agriculture on species abundance and composition of a tropical deciduous forest. Forest Ecology and Management 103:191–201.

Mills, A. M. 2005. Can breeding habitat be sexually selected? Auk 122:689–700.

Miranda, F., and E. Hernandez. 1963. Los tipos de vegetacion de Mexico y su clasificacion. Boletin de la Sociedad Botanica de Mexico 28:29–179.

Mittermeier, R. A. 1988. Primate diversity and the tropical forest. Pages 145–154 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D. C., USA.

Mittermeier, R. A., P. Robles Gil, and C. G. Mittermeier. 1997. Megadiversity: Earth's biologically wealthiest nations. CEMEX, Mexico City, Mexico.

Mizutani, H., M. Fukuda, Y. Kabaya, and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403.

Moller, A. P. 2004. Protandry, sexual selection, and climate change. Global Change Biology 10:2028–2035.

Moller, A. P. 2007. Tardy females, impatient males: protandry and divergent selection on arrival date in the two sexes of the barn swallow. Behavioral Ecology and Sociobiology 61:1311–1319.

Moller, A. P., and T. R. Birkhead. 1994. The evolution of plumage brightness in birds in related to extrapair paternity. Evolution 48:1089–1100.

Moller, A. P., and F. de Lope. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. Evolution 48:1676–1683.

Moller, A. P., and T. Szep. 2005. Rapid evolutionary change in a secondary sexual character linked to climate change. Journal of Evolutionary Biology 18:481–495.

Moore, R. T. 1938. Unusual birds and extensions of ranges in Sonora, Sinaloa, and Chihuahua, Mexico. Condor 40:23–28.

Morales, M. B., V. Bretagnolle, and B. Arroyo. 2005. Viability of the endangered little bustard *Tetrax tetrax* population of western France. Biodiversity and Conservation 14:3135–3150.

Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. University of Wisconsin Press, Madison, USA.

Morrow, E. H., and T. E. Pitcher. 2003. Sexual selection and the risk of extinction in birds. Proceedings of the Royal Society of London Series B 270:1793–1799.

Morse, D. H. 1976. Variables determining the density and territory size of breeding spruce-woods warblers. Ecology 57:290–301.

Morse, D. H. 1980. Population limitation: breeding or wintering grounds? Pages 505–516 *in* A. Keast and E. S. Morton, editors. Migrants in the Neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Morton, E. S. 1980. Adaptations to seasonal changes by migrant land birds in the Panama Canal Zone. Pages 437–453 *in* A. Keast, and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C., USA.

Morton, E. S. 1990. Habitat segregation by sex in the hooded warbler: experiments on proximate causation and discussion of its evolution. American Naturalist 135:319–333.

Morton, E.S. 1992. What do we know about the future of migrant landbirds? Pages 579–589 *in* J.M. Hagan III and D.W. Johnston, Editors, Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Morton, E. S., J. F. Lynch, K. Young, and P. Mehlhop. 1987. Do male hooded warblers exclude females from non-breeding territories in tropical forest? Auk 104:133–135.

Morton, G. A., and M. L. Morton. 1990. Dynamics of postnuptial molt in free-living mountain white-crowned sparrows. Condor 92:813–828.

Murphy, M. E., and J. R. King. 1992. Nutritional aspects of avian molt. Proceedings of the International Ornithological Congress 20:2186–2194.

Murphy, M. T., A. Pierce, J. Shoen, K. L. Murphy, J. A. Campbell, and D. A. Hamilton. 2001. Population structure and habitat use by overwintering Neotropical migrants on a remote oceanic island. Biological Conservation 102:333–345.

Murphy, P. G., and A. E. Lugo. 1986. The ecology of tropical dry forest. Annual Review of Ecology and Systematics 17:67–88.

Murphy, P. G., and A. E. Lugo. 1995. Dry forests of Central America and the Caribbean. Pages 9–34 *in* S. H. Bullock, H. A. Mooney, and E. Medina, editors. Seasonally dry tropical forests. Cambridge University Press, Cambridge, United Kingdom.

Musgrave, M. L., and J. L. Banner. 1993. Regional ground-water mixing and the origin of saline fluids: midcontinent, United States. Science 259:1877–1882.

Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology 59:1527–1534.

Myers, J. P., R. I. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner, and A. Tarak. 1987. Conservation strategies for migratory species. American Scientist 75:18–26.

National Oceanographic and Atmospheric Administration [NOAA]. National Climatic Data Center. 2013. Climate Data Online. <https://www.ncdc.noaa.gov/cdo-web/>. Accessed 15 September 2013.

Nichols, W. F., K. T. Killinbeck, and P. V. August. 1998. The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. Conservation Biology 12:371–379.

Nilsson, J.-A., and E. Svensson. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London Series B 263:711–714.

Nixon, K. C. 1993. The genus *Quercus* in Mexico. Pages 447–458 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, USA.

Nixon, K. C. 2006. Global and Neotropical distribution and diversity of oak (genus *Quercus*) and oak forests. Pages 3–13 *in* M. Kappelle, editor. Ecology and conservation of Neotropical montane oak forests. Springer-Verlag, Berlin, Germany.

Nomaru, T. 2002. Effective size of populations with unequal sex ratio and variation in mating success. Journal of Animal Breeding and Genetics 119:297–310.

Norman, G. W., M. M. Conner, J. C. Pack, and G. C. White. 2004. The effects of fall hunting on survival of male wild turkeys in Virginia and West Virginia. Journal of Wildlife Management 68:393–404.

Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American redstart (*Setophaga ruticilla*). Ornithological Monographs 61:14–28.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproduction success in a migratory bird. Proceedings of the Royal Society of London Series B 271:59–64.

North, M. P., and J. H. Reynolds. 1996. Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. Journal of Wildlife Management 60:639–653.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

Nunez, H. M., L. F. Rodriguez, and M. Khanna. 2011. Agave for tequila and biofuels: an economic assessment and potential opportunities. Global Change Biology Bioenergy 3:43–57.

Oberholser, H. C. 1974. The bird life of Texas. Volume 2. E. Kincaid, editor. University of Texas Press, Austin, USA.

Odeen, A., and O. Hastaad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 Opsin from total DNA. Molecular Biology and Evolution 20:855–861.

Orejuela, J. E., R. J. Raitt, and H. Alvarez. 1980. Differential use by North American migrants of three types of Columbian forest. Pages 253–264 *in* A. Keast, and E. S. Morton, editors. Migrant birds in the Neotropics. Smithsonian Institution Press, Washington, D. C., USA.

Parrish, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.

Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American redstarts wintering in Jamaica: importance of resource seasonality. Auk 111:38–49.

Peach, W. J., S. R. Baillie, and L. G. Underhill. 1991. Survival of British sedge warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. Ibis 133:300–305.

Pechacek, P. 2006. Foraging behavior of Eurasian three-toed woodpeckers (*Picoides tridactylus alpines*) in relation to sex and season in Germany. Auk 123:235–246.

Peek, K. M. 1989. Tree species preferences shown by foraging birds in forest plantations in northern England. Biological Conservation 48:41–57.

Pennington, R. T., M. Lavin, D. E. Prado, C. A. Pendry, S. K. Pell, and C. A. Butterworth. 2004. Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philosophical Transactions of the Royal Society B-Biological Sciences 359:515–537.

Pennington, R. T., D. A. Prado, and C. Pendry. 2000. Neotropical seasonally dry forest and Pleistocene vegetation changes. Journal of Biogeography 27:261–273.

Peralta-Hernandez, A. R., R. C. Balling, Jr., and L. R. Barba-Martinez. 2008. Analysis of near-surface diurnal temperature variations and trends in southern Mexico. International Journal of Climatology 29:205–209.

Peralta-Hernandez, A. R., R. C. Balling, Jr., and L. R. Barba-Martinez. 2009. Comparative analysis of indices of extreme rainfall events: variations and trends from southern Mexico. Atmosfera 22:219–228.

Perez, A., J. F. Mas, A. Velazquez, and L. Vazquez. 2008. Modeling vegetation diversity types in Mexico based upon topographic features. Interciencia 33:88–95.

Peterjohn, G. G., J. R. Sauer, and C. S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3-39 *in* T. E. Martin, and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, USA.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Petit, D. R., J. F. Lynch, R. L. Hutto, J. G. Blake, and R. B. Waide. 1995. Habitat use and conservation in the Neotropics. Pages 145–197 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, USA.

Phillips, J. C. 1911. A year's collecting in the state of Tamaulipas, Mexico. Auk 28:67–89.

Phillips, R. A., J. R. D. Silk, B. Phalan, P. Catry, and J. P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proceedings of the Royal Society of London Series B 271:1283–1291.

Pianka, E. R. 2000. Evolutionary ecology. Addison Wesley Longman, San Francisco, California, USA.

Pierce, K. B., Jr., T. Lookingbill, and D. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20:137–147.

Post, P., and F. Gotmark. 2006. Foraging behavior and predation risk in male and female Eurasian blackbirds (*Turdus merula*) during the breeding season. Auk 123:162–170.

Poulin, B., G. Lefebvre, and R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73:2295–2309.

Poulin, B., G. Lefebvre, and R. McNeil. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. Ibis 135:432–441.

Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society of London Series B 250:143–150.

Promislow, D. E., R. Montgomerie, and T. E. Martin. 1994. Sexual selection and survival in North American waterfowl. Evolution 48:2045–2050.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California, USA.

Rainio, K., A. P. Tottrup, E. Lehikoinen, and T. Coppack. 2007. Effects of climate change on the degree of protandry in migratory songbirds. Climate Research 35:107–114.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Report PSW-GTR-144. USDA Forest Service Pacific Southwest Research Station, Albany, California, USA.

Rappole, J. H. 1995. The ecology of migrant birds: a Neotropical perspective. Smithsonian Institution Press, Washington, D. C., USA.

Rappole, J. H., D. I. King, and W. Barrow. 1999. Winter ecology of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). Condor 101:762–770.

Rappole, J. H., D. I. King, and P. Leimgruber. 2000. Winter habitat and distribution of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). Animal Conservation 2:45–59.

Rappole, J. H., E. S. Morton, and M. A. Ramos. 1992. Density, philopatry, and population estimates for songbird migrants wintering in Veracruz. Pages 337–344 *in* J.M. Hagan, III, and D.W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 *in* A. E. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C., USA.

Ratzlaff, A. 1987. Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. Federal Register 52:37420–37423.

Redford, K. H., A. Taber, and J. A. Simonetti. 1990. There is more to biodiversity than tropical rain forests. In defense of non-rain forests ecosystems. Conservation Biology 4:1–3.

Reichlin, T. S., K. A. Hobson, L. I. Wassenaar, M. Schaub, D. Tolkmitt, D. Becker, L. Jenni, and R. Arlettaz. 2010. Migratory connectivity in a declining bird species: using feather isotopes to inform demographic modelling. Diversity and Distributions 16:643–654.

Renardo, J. 1886. Notes on some birds of the United States which occur in the Mexican fauna. Ornithologist and Oologist 11:132–133.

Rickers, M., I. Ramirez-Krauss, G. Ibarra-Manriquez, E. Martinez, C. H. Ramos, G. Gonzalez-Medellin, G. Gomez-Rodriguez, J. L. Palacio-Prieto, and H. M. Hernandez. 2007. Optimizing conservation of forest diversity: a country-wide approach in Mexico. Biodiversity and Conservation 16:1927–1957.

Ricklefs, R. E. 1992. The megapopulation: a model of demographic coupling between migrant and resident landbird populations. Pages 537–548 *in* J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Rimmer, C. 1988. Timing of the definitive pre-basic molt in yellow warblers at James Bay, Ontario. Condor 90:141–156.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences, USA 86:7658–7662.

Robinson, S. K. 1992. Population dynamics of breeding birds in a fragmented Illinois landscape. Pages 408–418 *in* J.M. Hagan, III, and D.W. Johnson, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Rockwell, S. M., C. I. Bocetti, and P. P. Marra. 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). Auk 129:744–752.

Rohwer, S. L. 2013. Molt intensity and conservation of a molt migrant (*Passerina ciris*) in northwest Mexico. Condor 115:421–433.

Rohwer, S. L., and G. S. Butcher. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. American Naturalist 131:556–572.

Rohwer, S., L. K. Butler, and D. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: ecology and evolution of migratory birds. Johns Hopkins University Press, Baltimore, Maryland, USA.

Rohwer, S., S. D. Fretwell, and D. M. Niles. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. American Naturalist 115:400–437.

Rohwer, S., K. A. Hobson, and V. G. Rohwer. 2009. Migratory double breeding in Neotropical migrant birds. Proceedings of the National Academy of Sciences, 26 October 2009, doi:10.1073/pnas.0908121106.

Rohwer, S. L., W. P. Klein Jr., and S. Heard. 1983. Delayed plumage maturation and the presumed prealternate molt in American redstarts (*Setophaga ruticilla*). Wilson Bulletin 95:199–208.

Romero-Duque, L. P., V. J. Jaramillo, and A. Perez-Jimenez. 2007. Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history. Forest Ecology and Management 253:38–47.

Rossmanith, E., V. Grimm, N. Blaum, and F. Jeltsch. 2006. Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*. Journal of Animal Ecology 75:540–548.

Rozanski, K., L. Araguas-Araguas, and R. Gonfiantini. 1992. Relation between long-term trends of oxygen-18 isotope composition of precipitation and climate. Science 258:981–985.

Rubinstein, D. R., C. P. Chamberlain, R. T. Holmes, M. P. Ayres, J. R. Waldbauer, G. R. Graves, and N. C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. Science 295:1062–1065.

Rubolini, D., F. Spina, and N. Saino. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. Behavioral Ecology 15:592–601.

Rundel, P. W., J. R. Ehleringer, and K. A. Nagy, editors. 1988. Stable isotopes in ecological research. Springer, Berlin, Germany.

Russell, S. M., and G. Morrison. 1996. The birds of Sonora. University of Arizona Press, Tucson, USA.

Rzedowski, J. 1978. Vegetacion de Mexico. Limusa, Distrito Federal, Mexico. [In Spanish.]

Rzedowski, J. 1991a. Diversidad y origenes de la flora fanerogamica de Mexico. Acta Botanica Mexicana 14:3–21.

Rzedowski, J. 1991b. El endemismo en la flora fanerogamica Mexicana: una apreciacion analitica preliminar. Acta Botanica Mexicana 15:47–64.

Rzedowski, J., and G. Calderon. 1987. El bosque tropical caudifolio de la region Mexicana del Bajio. Trace 12:12–21.

Saenz-Romero, C., G. E. Rehfeldt, N. L. Crookston, P. Duval, R. St-Amant, J. Beaulieu, and B. A. Richardson. 2010. Spline models of contemporary, 2030, 2060, and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. Climate Change 102:595–623.

Saenz-Romero, C., E. Snively, and R. Lindig-Cisneros. 2003. Conservation and restoration of pine forest genetic resources in Mexico. Silva Genetica 52:233–237.

Saino, N., T. Szep, M. Romano, D. Rubolini, F. Spina, and A. P. Moler. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters 7:21–25.

Sanchez-Azofeifa, G. A., M. Quesada, P. Cuevas-Reyes, A. Castillo, and G. Sanchez-Montoya. 2009. Land cover and conservation in the area of influence of the Chamela-Cuixmala Biosphere Reserve, Mexico. Forest Ecology and Management 258:907–912.

Sanchez-Azofeifa, G. A., M. Quesada, J. P. Rodriguez, J. M. Nassar, K. E. Stoner, A. Castillo, T. Garvin, E. L. Zent, J. C. Calvo-Alvarado, M. E.R. Kalacska, L. Fajardo, J. A. Gamon, and P. Cuevas-Reyes. 2005. Research priorities for Neotropical dry forests. Biotropica 37:477–485.

Sauer, J. R., and W. A. Link. 2011. Analysis of North American breeding bird survey using hierarchical models. Auk 128:87–98.

Schaldach, W. J., Jr. 1963. The avifauna of Colima and adjacent Jalisco, Mexico. Proceedings of the Western Foundation of Vertebrate Zoology 1:1–100.

Schmidt, P. M., R. A. McCleery, R. R. Lopez, N. J. Silvy, and J. A. Schmidt. 2010. Habitat succession, hardwood encroachment and raccoons as limiting factors for Lower Keys marsh rabbits. Biological Conservation 143:2703–2710.

Schwartz, P. 1980. Some considerations on migratory birds. Pages 31–34 *in* A. Keast, and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C., USA.

Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT]. 2002. Programa estrategico para conserver los ecosistemas y su biodiversidad. Secretaria de Medio Ambiente y Recursos Naturales. <http://www.ordenjuridico.gob.mx/Publicaciones/CDs2006/CDAmbiente/pdf/P6B.pdf>. Accessed 9 February 2012.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

Sellick, M. J., T. K. Kyser, M. B. Wunder, D. Chipley, and D. R. Norris. 2009. Geographic variation of strontium and hydrogen isotopes in avian tissue: implications for tracking migration and dispersal. PLoS ONE 4:e4735.

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defenses and trade-offs in evolutionary ecology. Trends in Ecology and Evolution 11:317–321.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? Pages 85-120 *in* T. E. Martin, and D.M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, Oxford, United Kingdom.

Sherry, T. W., and R. T. Holmes. 1997. American redstart (*Setophaga ruticilla*). Account 277 *in* A. Poole and F. Gill, editors. The birds of North America, The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C., USA.

Sherry, T. W., M. D. Johnson, and A. M. Strong. 2005. Does winter food limit populations of migratory birds? Pages 414–425 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: ecology and evolution of migratory birds. Johns Hopkins University Press, Baltimore, Maryland, USA.

Shull, A. M. 1986. Endangered and threatened wildlife and plants: proposal to determine the black-capped vireo to be an endangered species. Federal Register 51:44808–44812.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2010. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91:2874–2882.

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2011. Influence of moisture and food supply on the movement dynamics of a nonbreeding migratory bird (*Parkesia noveboracensis*) in a seasonal landscape. Auk 128:43–52.

Smith, R. J., and F. R. Moore. 2005. Arrival time and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Sorci, G., A. P. Moller, and J. Clobert. 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. Journal of Animal Ecology 67:263–269.

Spottiswoode, C., A. P. Tottrup, and T. Coppack. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. Proceedings of the Royal Society of London B Series 273:3023–3029.

Sternberg, L. O., M. J. Deniro, and H. B. Johnson. 1984. Isotope ratios of cellulose from plants having different photosynthetic pathways. Plant Physiology 74:557–561.

Sternberg, L. S. L. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. Stable Isotopes in Ecological Research 68:124–141.

Sternberg, M., and M. Shoshany. 2001. Influence of slope aspect on Mediterranean woody formations: comparison of a semi-arid and an arid site in Israel. Ecological Research 16:335–345.

Stoddard, C. H., and G. M. Stoddard. 1987. Essentials of forest practice. Fourth edition. John Wiley and Sons, New York, USA.

Stouffer, P. C., and G. M. Dwyer. 2003. Sex-biased winter distribution and timing of migration of hermit thrushes (*Catharus guttatus*) in eastern North America. Auk 120:836–847.

Strong, A. A., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883–895.

Strong, A. A., and T. W. Sherry. 2001. Body condition of Swainson's warblers wintering in Jamaica and the conservation value of Caribbean dry forests. Wilson Bulletin 113:410–418.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115–122.

Studds, C. E., and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society of London Series B 278:3437–3443.

Suzaki, T., A. Kume, and Y. Ino. 2005. Effects of slope and canopy trees on light conditions and biomass of dwarf bamboo under a coppice canopy. Journal of Forest Resources 10:151–156.

Swaddle, J. P., M. S. Witter, I. C. Cuthill, A. Budden, and P. McCowen. 1996. Plumage condition affects flight performance in common starlings: implications for developmental homeostasis, abrasion and molt. Journal of Avian Biology 27:103–111.

Szekely, T., G. H. Thomas, and I. C. Cuthill. 2006. Sexual conflict, ecology and breeding systems in birds. Bioscience 56:801–808.

Tazik, D. J. 1991. Proactive management of an endangered species on army lands: the black-capped vireo on the lands of Fort Hood, Texas. Dissertation, University of Illinois, Urbana-Champaign, USA.

Tazik, D. J., and J. D. Cornelius. 1993. Status of the black-capped vireo at Fort Hood, Texas. Vol. III: population and nesting ecology. U.S. Army Construction Engineering Research Laboratories Technical Report EN-94/01 Champaign, Illinois, USA.

Terborgh, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey, USA.

Terborgh, J. 1992. Why American songbirds are vanishing. Scientific American 266:56–62.

Terrill, S. B., and K. P. Able. 1988. Bird migration terminology. Auk 105:205–206.

Terrill, S. B., and P. Berthold. 1989. Experimental evidence for endogenously programmed differential migration in the blackcap (*Sylva atricapilla*). Experientia 45:207–209.

Terrill, S. B., and P. Berthold. 1990. Ecophysiological aspects of rapid population growth in a novel migratory blackcap (*Sylva atricapilla*) population: an experimental approach. Oecologia 85:266–270.

Texas State Climatologist. 2013. Texas Normals Data. <http://climatexas.tamu.edu/index.php/data/texas-normals-data>. Accessed 14 September 2013.

Thiollay, J. M. 1988. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17–30.

Thomas, D. L., and E. J. Taylor. 2006. Study design and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

Thompson, C. W. 1991. The sequence of molts and plumages in painted buntings and implications for theories of delayed plumage maturation. Condor 93:209–235.

Tieszen, L. L., and T. W. Boutton. 1988. Stable isotopes in terrestrial ecosystem research. Pages 167-195 *in* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, editors. Stable isotopes in ecological research. Springer, Berlin, Germany.

Toledo, V. M., and M. de J. Ordonez. 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats. Pages 757-777 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, USA.

Torres-Dowdall, J., A. H. Farmer, E. H. Bucher, R. O. Rye, and G. Landis. 2009. Population variation in isotopic composition of shorebird feathers: implications for determining molting grounds. Waterbirds 32:300–310.

Tottrup, A. P., and K. Thorup. 2008. Sex-differentiated migration patterns, protandry, and phenology in North European songbird populations. Journal of Ornithology 149:161–167.

Trejo, I. 1998. Distribucion y diversidad de selvas bajas de Mexico: relaciones con el clima y el suelo. Thesis, Universidad Nacional Autonóma de México, Mexico. [In Spanish.]

Trejo, I. 1999. El clima de la selva baja caducifolia en Mexico. Investigaciones Geograficas 39:40–52.

Trejo, I., and R. Dirzo. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. Biological Conservation 94:133–142.

Trejo, I., and R. Dirzo. 2002. Floristic diversity of Mexican seasonally dry tropical forests. Biodiversity and Conservation 11:2063–2048.

Urban, D. L., C. Miller, P. N. Halpin, and N. L. Stephenson. 2000. Forest gradient response in Sierran landscapes: the physical template. Landscape Ecology 15:603–620.

U.S. Fish and Wildlife Service. 1991. Black-capped Vireo (*Vireo atricapillus*) recovery plan. United States Fish and Wildlife Service, Austin, Texas, USA.

U.S. Fish and Wildlife Service. 1996. Black-capped vireo population and habitat viability assessment report. C. Beardmore, J. Hatfield, and J. Lewis, editors, September 18-21, 1995 Workshop. Austin, Texas. U. S. National Biological Service Grant No. 80333-1923.

U. S. Fish and Wildlife Service. 2007. 5-year review: summary and evaluation of black-capped vireo (*Vireo atricapilla*). Endangered Species Bulletins and Technical Reports Paper 25. United States Fish and Wildlife Service, Arlington, Texas, USA.

van der Have, T. M. 1991. Conservation of Palearctic-African migrants: are both ends burning? Trends in Ecology and Evolution 6:308–310.

Van Hoose, S. G. 1955. Distributional and breeding records of some birds from Coahuila. Wilson Bulletin 67:302–303.

Vasquez, J. A., and T. J. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. Journal of Ecology 86:999–1020.

Vega Rivera, J. H., M. A. Ortega-Huerta, S. Sarkar, and J. H. Rappole. 2010. Modelling the potential winter distribution of the endangered black-capped vireo (*Vireo atricapilla*). Bird Conservation International 21:92–106.

Verhulst, S., S. J. Dieleman, and H. K. Parmentier. 1999. A tradeoff between immunocompetence and sexual ornamentation in domestic fowl. Proceedings of the National Academy of Sciences 96:4478–4481.

Vidal, R. M., C. Macias-Caballero, and C. D. Duncan. 1994. The occurrence and ecology of the golden-cheeked warbler in the highlands of northern Chiapas, Mexico. Condor 96:684–691.

Villers-Ruiz, L., and I. Trejo-Vasquez. 1998. Climate change on Mexican forests and natural protected areas. Global Environmental Change 8:141–157.

Vizza, C., B. L. Sanderson, D. G. Burrows, and J. J. Coe. 2013. The effects of ethanol preservation on fish fin stable isotopes: does variation in C:N ratio and body size matter? Transactions of the American Fisheries Society 142:1469–1476.

Vogiatzakis, I. N., G. H. Griffiths, and A. M. Mannion. 2003. Environmental factors and vegetation composition, Lefka Ori massif, Crete, S. Aegean. Global Ecology and Biogeography 12:131–146.

Vose, J. M., and J. M. Maass. 1999. A comparative analysis of hydrologic responses of tropical deciduous and temperate deciduous watershed ecosystems to climatic change. Pages 292–298 *in* C. Aguirre-Bravo and C. Rodriguez-Franco, editors. Proceedings of the North American Science Symposium: Toward a Unified Framework for Inventorying and Monitoring Forest Ecosystem Resources. RMRS-P-12. USDA Forest Service, Guadalajara, Mexico.

Waite, T. A., and P. G. Parker. 1997. Extrapair paternity and the effective size of socially monogamous populations. Evolution 51:620–621.

Wang, Y., and D. M. Finch. 2002. Consistency of mist netting and point counts in assessing landbird species richness and relative abundance during migration. Condor 104:59–72.

Wassenaar, L. I., and K. A. Hobson. 2000. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. Ecological Applications 10:911–916.

Wauer, R. H., and J. D. Ligon. 1977. Distributional relations of breeding avifauna of four southwestern mountain ranges. Pages 567–578 *in* R. H. Wauer and D. H. Riskind, editors. Transactions of the symposium on the biological resources of the Chihuahua Desert Region, United States and Mexico. U. S. Department of Interior, National Park Service.

Weatherhead, P. J., R. Montgomerie, H. L. Gibbs, and P. T. Boag. 1994. The cost of extra-pair fertilizations to female red-winged blackbirds. Proceedings of the Royal Society of London Series B 258:315–320.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds; the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Werner, R. A., and W. A. Brand. 2001. Referencing strategies and techniques in stable isotope ratio analysis. Rapid Communications in Mass Spectrometry 15:501–519.

Western Regional Climate Center. 2013. PRISM Precipitation Maps: 1961-90. <http://www.wrcc.dri.edu/precip.html>. Accessed 15 September 2013.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, F. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrack. 1981. Effects of forest fragmentation on the avifauna of the eastern deciduous forest. Pages 125-205 *in* R. L. Burgess, and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, USA.

Wiegmann, D. D., and T. Nguyen. 2006. Mating system and demographic constraints on the opportunity for sexual selection. Theoretical Population Biology 69:34–47.

Wilcove, D. S., and S. K. Robinson. 1990. The impact of forest fragmentation on bird communities in eastern North America. Pages 319–331 *in* A. Keast, editor.

Biogeography and ecology of forest bird communities. SPB Academic Publishing, The Hague, Netherlands.

Wilkins, N., R. A. Powell, A. A. T. Conkey, and A. G. Snelgrove. 2006. Population status and threat analysis for the black-capped vireo. Prepared for the U.S. Fish and Wildlife Service, Region 2.

Willis, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187–231.

Wilsey, C. B., J. J. Lawler, and D. A. Cimprich. 2012. Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. Remote Sensing of Environment 119:35–42.

Wolda, H., and S. J. Wright. 1992. Artificial dry season rain and its effects on tropical insect abundance and seasonality. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen 95:535–548.

Woolfenden, B. E., H. L. Gibbs, and S. G. Sealy. 2001. Demography of brown-headed cowbirds at Delta Marsh, Manitoba. Auk 118:156–166.

Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. Oecologia 144:607–617.

Wunderle, J. M. 1992. Sexual habitat segregation in wintering black-throated blue warblers in Puerto Rico. Pages 299–307 *in* J. M. Hagan, III, and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C., USA.

Wunderle, J. M. Jr., and R. B. Waite. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Condor 95:904–933.

Yeakley, J. A., G. M. Hornberger, W. T. Swank, P. V. Bolstad, and J. M. Vose. 2000. Soil moisture modelling in humid mountainous landscapes. Pages 205–224 *in* J. P. Wilson and J. C. Gallant, editors. Terrain analysis: principles and applications. Wiley, New York, USA.

Ziegler, H. 1989. Hydrogen isotope fractionation in plant tissues. Stable Isotopes in Ecological Research 68: 105–123.

Zink, R. M., A. W. Jones, C. C. Farquhar, M. C. Westberg, J. I. Gonzalez Rojas. 2010. Comparison of molecular markers in the endangered black-capped vireo (*Vireo atricapilla*) and their interpretation in conservation. Auk 127:797–806.

APPENDIX A

LOCATION RECORDS OF ALL BLACK-CAPPED VIREOS AT WINTER STUDY SITES IN MEXICO

No.	Date	State[1]	Study Site	Latitude (DD)	Longitude (DD)	Age/Sex[2]	Elevation (m)	Vegetation Type
1	7 Feb 2002	NAY	La Bajada, San Blas	21.50869	-105.14558	AM	329	Tropical semi-deciduous forest
2	17 Feb 2002	NAY	Santa Maria del Oro	21.37855	-104.56242	FJ	750	Tropical deciduous forest
3	17 Feb 2002	NAY	Santa Maria del Oro	21.37874	-104.56233	AM	781	Tropical deciduous forest
4	19 Feb 2002	NAY	Santa Maria del Oro	21.63833	-104.56028	AM	765	Riparian gallery forest
5	23 Feb 2002	NAY	Sayulita	20.85533	-105.44811	FJ	64	Tropical semi-deciduous forest
6	5 Mar 2002	JAL	Sierra de Manantlán	19.70347	-104.38283	FJ	1515	Mixed oak forest
7	23 Mar 2002	COL	Finca de San Antonio	19.42854	-103.69853	FJ	1445	Tropical semi-deciduous forest
8	23 Mar 2002	COL	Finca de San Antonio	19.42827	-103.69873	AM	1442	Tropical semi-deciduous forest
9	23 Mar 2002	COL	Finca de San Antonio	19.43267	-103.69824	FJ	1406	Tropical semi-deciduous forest
10	6 Feb 2003	SIN	Panuco Road, Copala	23.40853	-105.93262	AM	600	Tropical deciduous forest
11	8 Feb 2003	SIN	La Noria, Mazatlan	23.44522	-106.32653	AM	212	Thorn forest
12	21 Feb 2003	SIN	Hwy 5-03, Mazatlan	23.34597	-106.44315	AM	41	Thorn forest
13	25 Feb 2003	SIN	La Noria, Mazatlan	23.44687	-106.32567	FJ	233	Thorn forest

No.	Date	State[1]	Study Site	Latitude (DD)	Longitude (DD)	Age/Sex[2]	Elevation (m)	Vegetation Type
14	1 Mar 2003	NAY	Singayta, San Blas	21.58083	-105.24033	FJ	8	Tropical semi-deciduous forest
15	5 Mar 2003	NAY	Cerro de San Juan	21.51917	-104.97197	AM	1057	Tropical deciduous forest
16	5 Mar 2003	NAY	Cerro de San Juan	21.51850	-104.97210	AM	1045	Tropical deciduous forest
17	10 Mar 2003	NAY	Santa Maria del Oro	21.35442	-104.56265	AM	780	Riparian gallery forest
18	11 Mar 2003	NAY	Santa Maria del Oro	21.37920	-104.56265	AM	793	Tropical deciduous forest
19	11 Mar 2003	NAY	Santa Maria del Oro	21.37920	-104.56265	FJ	793	Tropical deciduous forest
20	11 Mar 2003	NAY	Santa Maria del Oro	21.37802	-104.56207	FJ	755	Tropical deciduous forest
21	22 Mar 2003	JAL	Barranca el Choncho, Barra de Navidad	19.34012	-104.73852	FJ	496	Thorn forest
22	29 Mar 2003	COL	Finca de San Antonio	19.43238	-103.70190	AM	1390	Tropical semi-deciduous forest
23	8 Dec 2003	SIN	Panuco Road, Copala	23.40878	-105.93538	AM	633	Tropical deciduous forest
24	8 Dec 2003	SIN	Panuco Road, Copala	23.40837	-105.93235	AM	611	Tropical deciduous forest
25	9 Dec 2003	SIN	Copala	23.38968	-105.93703	FJ	547	Tropical semi-deciduous forest
26	10 Dec 2003	SIN	Copala	23.38968	-105.93703	FJ	541	Tropical semi-deciduous forest
27	11 Dec 2003	SIN	Copala	23.38813	-105.93540	FJ	560	Tropical semi-deciduous forest
28	13 Dec 2003	SIN	La Noria, Mazatlan	23.43398	-106.33275	AM	184	Thorn forest
29	14 Dec 2003	SIN	La Noria, Mazatlan	23.43398	-106.33275	FJ	184	Thorn forest

No.	Date	State[1]	Study Site	Latitude (DD)	Longitude (DD)	Age/Sex[2]	Elevation (m)	Vegetation Type
30	14 Dec 2003	SIN	La Noria, Mazatlan	23.43398	-106.33275	AM	184	Thorn forest
31	16 Dec 2003	SIN	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.39642	-106.61163	AM	376	Tropical deciduous forest
32	16 Dec 2003	DUR	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.40722	-105.93538	AM	633	Tropical deciduous forest
33	16 Dec 2003	DUR	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.40722	-105.93538	AM	633	Tropical deciduous forest
34	16 Dec 2003	DUR	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.40812	-105.97053	AM	633	Tropical deciduous forest
35	17 Dec 2003	SIN	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.40347	-106.60388	FJ	353	Tropical deciduous forest
36	17 Dec 2003	SIN	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.40347	-106.60388	AM	360	Tropical deciduous forest
37	18 Dec 2003	DUR	Reserva Ecológica del Mineral de Nuestra Señora, Cosalá	24.39440	-106.32058	AM	424	Tropical deciduous forest
38	24 Dec 2003	SIN	La Noria, Mazatlan	23.46183	-106.32443	AM	183	Thorn forest
39	6 Jan 2004	SIN	La Noria, Mazatlan	23.46178	-106.32438	AM	159	Thorn forest
40	8 Jan 2004	NAY	Singayta, San Blas	21.58750	-105.23333	AM	0	Tropical semi-deciduous forest

No.	Date	State[1]	Study Site	Latitude (DD)	Longitude (DD)	Age/Sex[2]	Elevation (m)	Vegetation Type
41	9 Jan 2004	NAY	La Bajada, San Blas	21.50000	-105.15056	FJ	324	Tropical semi-deciduous forest
42	10 Jan 2004	NAY	La Bajada, San Blas	21.51139	-105.15056	FJ	217	Tropical semi-deciduous forest
43	15 Jan 2004	NAY	La Bajada, San Blas	21.51500	-105.13389	AM	322	Tropical semi-deciduous forest
44	16 Jan 2004	NAY	Singayta, San Blas	21.56667	-105.24639	AM	25	Tropical semi-deciduous forest
45	20 Jan 2004	NAY	Cerro de San Juan	21.51723	-104.97253	AM	1079	Tropical deciduous forest
46	20 Jan 2004	NAY	Cerro de San Juan	21.51868	-104.97225	AM	1049	Tropical deciduous forest
47	22 Jan 2004	NAY	Cerro de San Juan	21.51365	-104.97022	AM	1099	Mixed oak forest
48	22 Jan 2004	NAY	Cerro de San Juan	21.51082	-104.97022	AM	1174	Pine-oak forest
49	23 Jan 2004	NAY	Sayulita	20.84325	-105.45237	AM	8	Tropical semi-deciduous forest
50	28 Jan 2004	NAY	Santa Maria del Oro	21.37920	-104.56265	FJ	792	Tropical deciduous forest
51	24 Jan 2004	NAY	Santa Maria del Oro	21.37740	-104.55980	AM	813	Tropical deciduous forest
52	24 Jan 2004	NAY	Santa Maria del Oro	21.37740	-104.55980	FJ	735	Tropical semi-deciduous forest
53	24 Jan 2004	NAY	Santa Maria del Oro	21.36803	-104.56007	FJ	741	Tropical semi-deciduous forest
54	29 Jan 2004	NAY	Santa Maria del Oro	21.37825	-104.56547	FJ	785	Tropical deciduous forest
55	29 Jan 2004	NAY	Santa Maria del Oro	21.37765	-104.56102	AM	794	Tropical deciduous forest
56	30 Jan 2004	NAY	Santa Maria del Oro	21.37510	-104.55832	FJ	714	Tropical semi-

No.	Date	State[1]	Study Site	Latitude (DD)	Longitude (DD)	Age/Sex[2]	Elevation (m)	Vegetation Type
								deciduous forest
57	31 Jan 2004	NAY	Santa Maria del Oro	21.00634	-104.54755	AM	696	Tropical deciduous forest
58	31 Jan 2004	NAY	Santa Maria del Oro	21.38010	-104.55125	AM	741	Tropical deciduous forest
59	2 Feb 2004	NAY	Santa Maria del Oro	21.36530	-104.58053	FJ	708	Tropical deciduous forest
60	5 Feb 2004	NAY	Santa Maria del Oro	21.36015	-104.57482	FJ	745	Tropical deciduous forest
61	10 Feb 2004	COL	Playa de Oro	19.15535	-104.50427	AM	113	Thorn forest
62	12 Feb 2004	JAL	Barranca el Choncho, Barra de Navidad	19.33912	-104.74145	FJ	373	Thorn forest
63	13 Feb 2004	COL	Microondas el Toro	19.13927	-104.45638	FJ	286	Thorn forest
64	15 Feb 2004	COL	Playa de Oro	19.15587	-104.50268	FJ	107	Thorn forest
65	15 Feb 2004	COL	Playa de Oro	19.15228	-104.50698	FJ	159	Thorn forest
66	18 Feb 2004	COL	Finca de San Antonio	19.43350	-103.69963	FJ	1437	Tropical semi-deciduous forest
67	18 Feb 2004	COL	Finca de San Antonio	19.43053	-103.70362	FJ	1358	Tropical semi-deciduous forest
68	19 Feb 2004	COL	Finca de San Antonio	19.43140	-103.69815	FJ	1462	Tropical semi-deciduous forest
69	20 Feb 2004	COL	Finca de San Antonio	19.43140	-103.69837	AM	1429	Tropical semi-deciduous forest
70	21 Feb 2004	COL	Finca de San Antonio	19.43848	-103.71070	FJ	1276	Tropical semi-deciduous forest
71	24 Feb 2004	COL	Finca de San Antonio	19.44315	-103.71407	AM	1196	Tropical semi-deciduous forest

[1] States of vireo observations include Colima (COL), Durango (DUR), Jalisco (JAL), Nayarit (NAY), and Sinaloa (SIN).
[2] Age/sex categories for individual vireos are: AM= adult male, FJ= female or juvenile.

APPENDIX B

BLACK-CAPPED VIREO FEATHER STABLE ISOTOPE DATA FROM BREEDING AND WINTERING SITES, INCLUDING DEUTERIUM (δ^2H), CARBON (δ^{13}C), AND NITROGEN (δ^{14}N)

NO.	DATE	STATE[1]	STUDY SITE	PROVIDER[2]	δ^2H (‰)	δ^{13}C (‰)	δ^{14}N (‰)
1	4/19/1910	COA	Sabinas	MVZ	-68.2	-21.48	7.30
2	4/23/1953	COA	Sierra del Carmen	MVZ	-57.1	-22.27	9.63
3	4/26/1953	COA	Sierra del Carmen	MVZ	-23.7	-19.77	6.73
4	4/24/1953	COA	Sierra del Carmen	MVZ	-52.3	-21.03	7.02
5	4/27/1953	COA	Sierra del Carmen	MVZ	-20.4	-19.50	6.51
6	4/23/1953	COA	Sierra del Carmen	MVZ	-30.6	-19.96	6.84
7	5/08/1954	COA	Sierra Padilla	KU	-42.4	-19.10	7.24
8	5/09/1954	COA	Sierra Padilla	KU	-34.9	-19.39	6.61
9	7/03/1952	COA	Sierra del Pino	KU	-31.2	-19.82	6.60
10	7/03/1952	COA	Sierra del Pino	KU	-57.4	-21.63	6.99
11	4/02/1910	COA	Sabinas	AMNH	-37.4	-20.64	8.10
12	6/18/1956	COA	Ocampo	FMNH	-44.8	-21.15	7.23
13	6/18/1956	COA	Ocampo	FMNH	-48.9	-21.97	6.55
14	6/17/1956	COA	Ocampo	FMNH	-95.4	-21.17	6.65
15	2/26/1904	COL	Coquimatlan	AMNH	-49.6	-20.32	6.01
16	2/08/1959	COL	Pueblo Juarez	DMNH	-95.8	-19.69	6.73
17	10/27/1957	COL	Manzanillo	MVZ	-48.1	-20.14	8.02
18	2/10/2004	COL	Playa de Oro	R. Powell	-43.2	-[3]	-
19	2/13/2004	COL	Microondas el Toro	R. Powell	-40.5	-	-
20	2/15/2004	COL	Play de Oro	R. Powell	-37.9	-21.71	7.50
21	2/20/2004	COL	La Maria	R. Powell	-38.2	-21.43	5.90
22	2/24/2004	COL	La Maria	R. Powell	-47.4	-22.55	7.08
23	10/21/1937	DUR	Rancho Guasimal	Moore Col.	-44.2	-19.55	7.64
24	11/13/1937	DUR	Rancho Guasimal	Moore Col.	-35.6	-20.98	8.63

NO.	DATE	STATE[1]	STUDY SITE	PROVIDER[2]	$\delta^{2}H$ (‰)	$\delta^{13}C$ (‰)	$\delta^{14}N$ (‰)
25	11/21/1937	DUR	Tamazula	Moore Col.	-26.7	-20.61	9.06
26	12/10/1937	DUR	Tamazula	Moore Col.	-44.6	-20.42	6.22
27	UNK. 1888	GUE	El Rincon	BMNH	-50.8	-22.22	8.39
28	1/12/1891	JAL	Unk.	AMNH	-84.9	-20.79	6.06
29	2/19/1952	JAL	Sapotillo	Moore Col.	-24.4	-19.57	5.28
30	2/21/1952	JAL	Sapotillo	Moore Col.	-24.9	-20.26	7.34
31	12/03/1956	JAL	Suchitlan	DMNH	-22.7	-19.34	6.63
32	3/24/2003	JAL	Barranca el Choncho	R. Powell	-69.5	-22.47	8.77
33	1/01/1953	MIC	Tiquichio	Moore Col.	-42.6	-21.02	8.96
34	8/27/1938	NAY	Tepic	Moore Col.	-55.2	-19.68	6.44
35	3/15/1941	NAY	Chacala	Moore Col.	-51.2	-20.56	7.26
36	3/19/1948	NAY	San Blas	Moore Col.	-34.4	-21.27	6.62
37	11/04/1957	NAY	San Blas	DMNH	-33.5	-20.29	7.36
38	11/28/1952	NAY	Las Veras	DMNH	-53.1	-20.72	5.94
39	11/25/1952	NAY	Las Varas	DMNH	-38.2	-19.74	6.05
40	11/16/1952	NAY	Las Varas	DMNH	-50.8	-20.41	8.98
41	10/08/1955	NAY	Tepic	DMNH	-37.6	-21.15	6.93
42	10/10/1957	NAY	San Blas	DMNH	-36.1	-20.12	7.04
43	11/30/1952	NAY	Compostela	DMNH	-28.5	-20.58	6.66
44	12/28/1955	NAY	Las Veras	FMNH	-34.9	-21.23	8.29
45	12/29/1955	NAY	Las Veras	FMNH	-52.4	-21.24	7.69
46	3/11/2003	NAY	Santa Maria del Oro	R. Powell	-54.4	-22.00	5.08
47	3/01/2003	NAY	Singayta	R. Powell	-43.0	-	-
48	3/06/2003	NAY	Cerro de San Juan	R. Powell	-74.7	-24.92	7.96
49	1/08/2004	NAY	Singayta	R. Powell	-51.2	-21.85	3.39
50	1/12/2004	NAY	La Bajada, San Blas	R. Powell	-69.7	-24.67	7.27
51	1/15/2004	NAY	La Bajada, San Blas	R. Powell	-41.1	-	-
52	1/16/2004	NAY	Singayta	R. Powell	-36.0	-21.78	3.03
53	1/20/2004	NAY	Cerro de San Juan	R. Powell	-53.4	-21.85	5.13
54	1/29/2004	NAY	Santa Maria del Oro	R. Powell	-31.3	-20.26	6.20
55	1/30/2004	NAY	Santa Maria del Oro	R. Powell	-46.4	-21.87	4.67
56	1/31/2004	NAY	Santa Maria del Oro	R. Powell	-56.9	-22.14	6.74

NO.	DATE	STATE[1]	STUDY SITE	PROVIDER[2]	$\delta^{2}H$ (‰)	$\delta^{13}C$ (‰)	$\delta^{14}N$ (‰)
57	1/31/2004	NAY	Santa Maria del Oro	R. Powell	-36.4	-20.33	5.71
58	2/01/2004	NAY	Santa Maria del Oro	R. Powell	-52.5	-	-
59	12/08/1963	OAX	San Gabriel Mixtepec	DMNH	-50.8	-21.55	8.37
60	12/11/1963	OAX	San Gabriel Mixtepec	DMNH	-59.2	-21.47	7.68
61	2/XX/1868	SIN	Mazatlan	USNM	-59.7	-21.60	12.94
62	12/18/1933	SIN	Rosario	Moore Col.	-60.7	-20.31	5.56
63	1/06/1934	SIN	Rosario	Moore Col.	-57.8	-20.44	7.70
64	2/26/1935	SIN	Rosario	Moore Col.	-34.2	-21.42	7.04
65	2/09/1935	SIN	Chele	Moore Col.	-36.8	-21.03	6.17
66	2/15/1935	SIN	Chele	Moore Col.	-54.8	-22.24	10.43
67	3/18/1937	SIN	San Ignacio	Moore Col.	-44.6	-21.23	5.75
68	3/20/1937	SIN	San Ignacio	Moore Col.	-60.5	-20.57	7.56
69	2/21/1938	SIN	Iguana	Moore Col.	-43.2	-21.38	5.73
70	4/12/1972	SIN	Palmito	DMNH	-71.6	-21.00	7.27
71	12/21/1955	SIN	Concordia	FMNH	-35.7	-20.79	9.43
72	2/21/2003	SIN	Mazatlan	R. Powell	-38.8	-	-
73	12/08/2003	SIN	Panuco Road	R. Powell	-56.1	-	-
74	12/10/2003	SIN	Copala	R. Powell	-43.1	-22.86	7.70
75	12/16/2003	SIN	Cosalá	R. Powell	-51.9	-22.75	6.45
76	12/16/2003	SIN	Cosalá	R. Powell	-53.6	-21.26	5.81
77	12/17/2003	SIN	Cosalá	R.Powell	-36.2	-20.63	5.32
78	1/06/2004	SIN	La Noria, Mazatlan	R. Powell	-57.5	-	-
79	7/04/2003	OKL	Fort Sill	J Grzybowski	-57.8	-	-
80	7/04/2003	OKL	Fort Sill	J Grzybowski	-70.5	-	-
81	7/08/2003	OKL	Fort Sill	J Grzybowski	-20.3	-25.82	7.07
82	7/11/2003	OKL	Fort Sill	J Grzybowski	11.6	-	-
83	7/11/2003	OKL	Fort Sill	J Grzybowski	-71.3	-24.37	8.07
84	7/11/2003	OKL	Fort Sill	J Grzybowski	-60.8	-	-
85	7/16/2003	OKL	Fort Sill	J Grzybowski	-78.9	-24.47	6.24
86	7/16/2003	OKL	Fort Sill	J Grzybowski	-49.2	-22.16	4.87
87	7/18/2003	OKL	Fort Sill	J Grzybowski	-52.5	-22.65	3.58
88	7/18/2003	OKL	Fort Sill	J Grzybowski	-50.7	-21.48	6.92

NO.	DATE	STATE[1]	STUDY SITE	PROVIDER[2]	$\delta^{2}H$ (‰)	$\delta^{13}C$ (‰)	$\delta^{14}N$ (‰)
89	7/20/2003	OKL	Fort Sill	J Grzybowski	-54.1	-23.42	3.06
90	7/20/2003	OKL	Fort Sill	J Grzybowski	-49.9	-22.45	5.00
91	7/21/2003	OKL	Fort Sill	J Grzybowski	-40.7	-23.00	6.82
92	7/21/2003	OKL	Fort Sill	J Grzybowski	-47.6	-22.69	3.48
93	7/21/2003	OKL	Fort Sill	J Grzybowski	-56.9	-21.89	3.64
94	7/22/2003	OKL	Fort Sill	J Grzybowski	-64.8	-	-
95	7/22/2003	OKL	Fort Sill	J Grzybowski	-62.1	-	-
96	7/22/2003	OKL	Fort Sill	J Grzybowski	-80.0	-	-
97	7/07/2003	OKL	Fort Sill	J Grzybowski	-75.5	-	-
98	7/20/2003	OKL	Fort Sill	J Grzybowski	-50.3	-	-
99	4/23/2003	TEX	Fort Hood	D. Cimprich	-27.9	-	-
100	7/15/2003	TEX	Fort Hood	D. Cimprich	-64.2	-	-
101	5/13/2003	TEX	Fort Hood	D. Cimprich	-87.3	-24.23	6.97
102	5/13/2003	TEX	Fort Hood	D. Cimprich	-39.1	-	-
103	7/10/2003	TEX	Fort Hood	D. Cimprich	-43.4	-20.85	6.37
104	5/27/2003	TEX	Fort Hood	D. Cimprich	-39.4	-	-
105	5/07/2003	TEX	Fort Hood	D. Cimprich	-94.0	-24.51	5.20
106	4/28/2003	TEX	Fort Hood	D. Cimprich	-87.4	-23.99	6.13
107	4/29/2003	TEX	Fort Hood	D. Cimprich	-48.4	-20.88	5.53
108	4/29/2003	TEX	Fort Hood	D. Cimprich	-44.7	-22.27	4.95
109	4/24/2003	TEX	Fort Hood	D. Cimprich	-80.4	-24.62	9.82
110	4/22/2003	TEX	Fort Hood	D. Cimprich	-44.6	-21.87	6.65
111	4/21/2003	TEX	Fort Hood	D. Cimprich	-86.5	-23.76	8.09
112	4/21/2003	TEX	Fort Hood	D. Cimprich	-	-22.01	4.63
113	4/16/2003	TEX	Fort Hood	D. Cimprich	-86.9	-	-
114	4/14/2003	TEX	Fort Hood	D. Cimprich	-	-22.38	3.77
115	4/26/2004	TEX	Fort Hood	D. Cimprich	-37.4	-20.62	4.72
116	6/25/2004	TEX	Fort Hood	D. Cimprich	-42.5	-21.09	5.15
117	5/06/2004	TEX	Fort Hood	D. Cimprich	-47.9	-	-
118	4/25/2004	TEX	Fort Hood	D. Cimprich	-100.1	-24.61	7.19
119	4/25/2004	TEX	Fort Hood	D. Cimprich	-38.0	-22.29	2.49
120	5/05/2004	TEX	Fort Hood	D. Cimprich	-91.8	-23.28	7.93

NO.	DATE	STATE[1]	STUDY SITE	PROVIDER[2]	$\delta^{2}H$ (‰)	$\delta^{13}C$ (‰)	$\delta^{14}N$ (‰)
121	5/17/2004	TEX	Fort Hood	D. Cimprich	-35.5	-22.13	7.68
122	6/16/2004	TEX	Fort Hood	D. Cimprich	-92.5	-23.39	6.02
123	4/27/2004	TEX	Fort Hood	D. Cimprich	-42.1	-20.55	5.08
124	4/27/2004	TEX	Fort Hood	D. Cimprich	-42.3	-21.12	5.52
125	6/24/2004	TEX	Fort Hood	D. Cimprich	-78.0	-23.43	9.05
126	5/17/2004	TEX	Fort Hood	D. Cimprich	-67.8	-22.39	8.76
127	5/28/2004	TEX	Fort Hood	D. Cimprich	-90.1	-23.83	5.19
128	6/01/2004	TEX	Fort Hood	D. Cimprich	-37.0	-20.67	6.36
129	4/25/2004	TEX	Fort Hood	D. Cimprich	-87.4	-24.35	8.71
130	4/25/2004	TEX	Fort Hood	D. Cimprich	-85.9	-22.99	7.01
131	4/07/2004	TEX	Fort Hood	D. Cimprich	-31.9	-22.56	4.19
132	6/11/2004	TEX	Fort Hood	D. Cimprich	-50.4	-20.91	6.50
133	UNK.	TEX	Fort Hood	D. Cimprich	-92.2	-	-
134	4/27/2004	TEX	Fort Hood	D. Cimprich	-73.2	-24.68	8.67
135	6/29/2004	TEX	Fort Hood	D. Cimprich	-90.1	-25.01	9.12
136	7/02/2004	TEX	Fort Hood	D. Cimprich	-54.2	-21.53	7.50
137	6/04/2004	TEX	Fort Hood	D. Cimprich	-82.4	-24.00	6.33
138	5/24/2004	TEX	Fort Hood	D. Cimprich	-88.5	-	-
139	5/24/2004	TEX	Fort Hood	D. Cimprich	-86.0	--25.40	8.12
140	4/29/2004	TEX	Fort Hood	D. Cimprich	-41.6	-21.75	6.51
141	5/20/2004	TEX	Fort Hood	D. Cimprich	-64.1	-24.13	9.26
142	6/17/2004	TEX	Fort Hood	D. Cimprich	-81.1	-24.77	9.03
143	UNK.	TEX	Fort Hood	D. Cimprich	-93.6	-24.53	7.94
144	5/03/2004	TEX	Fort Hood	D. Cimprich	-93.1	-24.92	7.65

1 States of feather collection include the Mexican states of Coahuila (COA), Colima (COL), Durango (DUR), Guerrero (GUE), Jalisco (JAL), Michoacán (MIC), Nayarit (NAY), Oaxaca (OAX), and Sinaloa (SIN), and the U.S. states of Oklahoma (OKL), and Texas (TEX).

2 Museum and research collections that provided samples of vireo feathers for analysis include the University of California, Berkeley Museum of Vertebrate Zoology (MVZ), the University of Kansas Natural History Museum (KU), the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), the Delaware Museum of Natural History (DMNH), the Moore Laboratory of Zoology at Occidental College (Moore Col.), the British Museum of Natural History (BMNC), and the Smithsonian Institution (USNM).

[3] Dashes (-) indicate data that is missing either due to insufficient quantity of tissue for analysis or due to processing error with that particular sample.